

FORM AND FUNCTION IN THE INTERPRETATION OF FEEDING IN LUMBRICID WORMS

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INTRODUCTION

THE prerequisite for survival demands that an organism must have a structural pattern which is consistent with the environment in which it finds itself. The success of such a pattern depends on the harmonious integration and regulation of its constituent parts both in response to changing conditions within itself and with those of the external environment. The organism, too, must possess the necessary attributes to utilize the resources of the environment at all levels, including the biochemical and the biophysical, so as to maintain its fundamental metabolic pathways. In the ultimate, however, the success of an organism depends on the completeness of a complex of conditions, which are superimposed on the basic pattern by the environment. To occur and survive in a given situation an organism must have essential materials for growth and reproduction. The basic requirements vary with the species and with the situation and, in agreement with Liebig's law of the minimum, the essential material available in amounts most closely approaching the critical limit needed will tend to be a limiting one. The absence or failure of an organism can be dictated not only by the qualitative or quantitative deficiency but by excess with respect to any one of several factors which may approach the limits of tolerance for that organism—i.e. too much of any one factor may also be inimical. So that organisms have an ecological minimum and maximum, and the intervening range represents the limits of tolerance. In brief, there is (a) a basic underlying morphological and physiological pattern to organisms which determines the broad type of habitat they can potentially colonize and (b) there are 'finer adjustments' within this situation which limit species to localized areas depending on the degree of ecological tolerance of the species concerned.

The approach in the present account has been limited to one aspect of the problem, viz. that of feeding in lumbricid worms, and this has involved a study of the relevant basic organization of a representative species and its associated complexities. This has provided a basis for a consideration of the relationships of the body forms of the Lumbricidae as an indirect means of determining the types of habitats which they can potentially exploit as suggested under (a) above. On this ability will depend their food getting habits as well as the return of essential minerals to the soil in the form of casts. Moreover, this information may prove to be of value in the application of criteria so frequently used in field studies as defined under (b) above. These concepts, sometimes speculative, because of lack of field data, may in addition to being of academic interest prove useful in assessing the intake of pesticides, applied to soils, by various worm species. Recently a report of the Research Committee on toxic chemicals¹ emphasized the need for more extended studies of the inter-relations of organisms in the soil and of the effects of pesticides in these inter-relations, and

that more work should be done in Britain on the possible accumulation of pesticide residues in soil animals.

The lumbricid worms, commonly referred to as earthworms, are represented in Britain by 37 species, varieties or forms belonging to 9 genera², and are listed at the end of this account. Of these, probably the best known are the genera *Lumbricus* and *Allolobophora* whose claim to fame rests on their being the introductory types to coelomatic organization in biological courses. Even so, the synecology of some species, notably those from pastures and moorlands, has been investigated by Evans³, Evans and Guild⁴⁻⁸, Guild⁹⁻¹², Satchell¹³⁻¹⁶ and Svendsen¹⁷⁻¹⁸ among others in Britain. In these papers the major considerations have been devoted either to population dynamics or to the 'finer adjustments' within habitats (or ecological tolerances of species) e.g. the relationship between distribution and pH values of the soil, and due attention has not been paid to the underlying organizational pattern of the animals.

GUT STRUCTURE

Basic problems. On purely mechanical grounds an animal whose movements are a function of altering body form, determined by changing internal pressures and associated muscular movements, requires to have compensating adjustments in its internal organization. Basically the worm is analogous to two tubes, one fitted within the other, the outer component representing the body wall, the inner the gut wall. The ends between the two tubes are closed off, leaving one opening which corresponds to the mouth of the worm, the other to its anus. Now if the outer body wall stretches, as does that of the worm, the inner one must continue to be accommodated. On mechanical grounds the following devices are possible: (a) the gut wall may be of the same length and thickness as the body wall and would stretch correspondingly, but one drawback of such an arrangement is that it would add considerably to the bulk of the animal and the gut would be unable to undergo peristaltic movements independently of the body wall; (b) the gut wall might be thin and of the same degree of extensibility and contractility as that of the body wall. The disadvantage of such a wall would be its inability to withstand the high hydrostatic pressures developed within the coelom when the outer wall was stretched, and conversely the improbability of the inner wall being able to withstand pressures exerted by the gut contents under pressure. Finally, as with a thick-walled gut, there is the impracticability of such a tube being able to undergo independent peristalsis. The third possibility (c) envisages a gut which, relative to the body wall, is longer and accommodated during the contracted phase by being thrown into folds. By this means the gut folds would partially unfold as the body wall stretched, but because the folds are not under tension the effects of the hydrostatic pressures would be reduced and independent peristaltic movement would be possible. It is this third possibility which occurs in earthworms.

Because of the body length relative to the circumference and the high pressures acting on the gut wall and generated by the circular body muscles through the coelomic fluid, the need arises for a force pump to supplement the weak peristaltic action of the gut in forcing food along the food tract. Such pumps in the gut of the worm are the pharynx and the gizzard. The evolution of a force pump requires devices to control the direction of flow of the food and

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to regulate the speed at which food moves along the tract, and this in the earthworm is supplied by valves.

The relationships between the prostomium, the peristomium and the mouth. One of the characters commonly used in separating the different genera of earthworms is the relationship which exists between the prostomium and the peristomium, when seen in dorsal view. If the prostomium is not separated from the peristomium by a transverse groove it is said to be zygotobous, and if separated by such a groove it is referred to as being prolobous. In some genera this transverse groove is interrupted on either side of the mid-dorsal line and from it two parallel anteroposterior grooves arise. Should such grooves extend to about midway along the peristomium, the prostomium is referred to as epilobous, and if reaching to the posterior margin of the peristomium as tanylobous. *Lumbricus terrestris*, on which the following description is based, is classified under this last group.

The visible portion of the prostomium is lobed and posteriorly is overlapped dorsolaterally, laterally and ventrally by the peristomium, i.e. the latter forms an incomplete annular ring, being broadest dorsolaterally on either side of the backward mid-dorsal extension of the prostomium and narrowest ventrally. Removal of the lateral wall of the peristomium and of the second segment, as shown in *Figure 7.1*, reveals an extensive proximal portion of the prostomium,

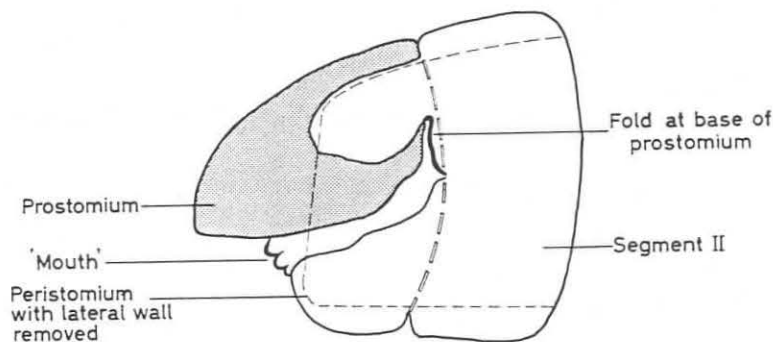


Figure 7.1. Side view of prostomium after the removal of the side wall of the peristomium

deeply intucked into the peristomium. The overall picture of the prostomium then consists of a median, dorsal, posterior continuation of the distal lobe separated on each side by a deep concavity from an even stronger and broader mid-ventral extension which reaches back almost to the posterior limit of the peristomium, where it becomes continuous with a deeply invaginated fold.

In transverse section the outline of the prostomium is oval distally; it has a very thick epidermis well supplied with photosensitive cells and the coelom is almost obliterated by oblique longitudinal muscles which originate from its dorsal and dorsolateral walls as well as in part from the longitudinal muscle bands of the peristomial segment. There are also present well defined transverse muscle bands dorsally, and lateral bands peripherally. Considerable connective tissue is present and many fine branches of the prostomial nerves are

visible. At about 20 to 40 μ from the anterior end the nerve fibrils run together to form the main branches of the prostomial nerves, and the muscles which were transverse at the tip now become arcuate.

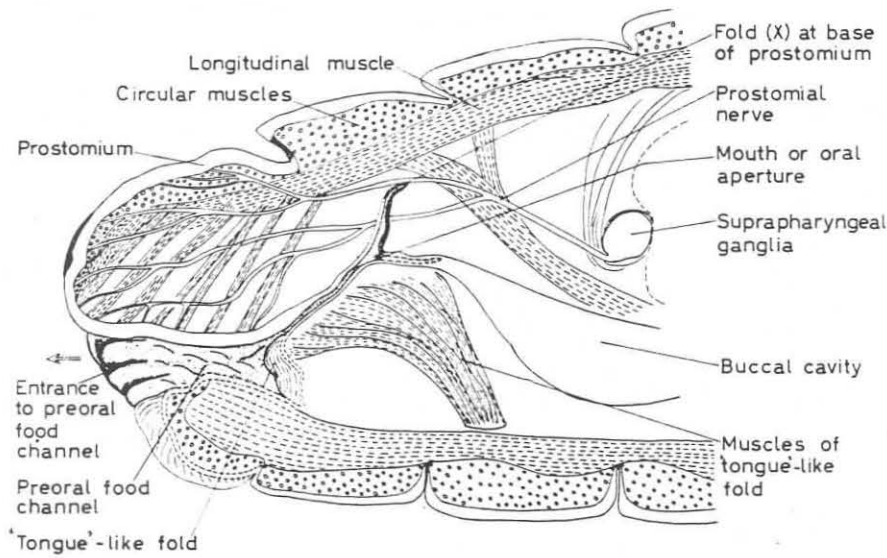


Figure 7.2a. Median sagittal section of the anterior end of *Lumbricus terrestris* with the prostomium retracted

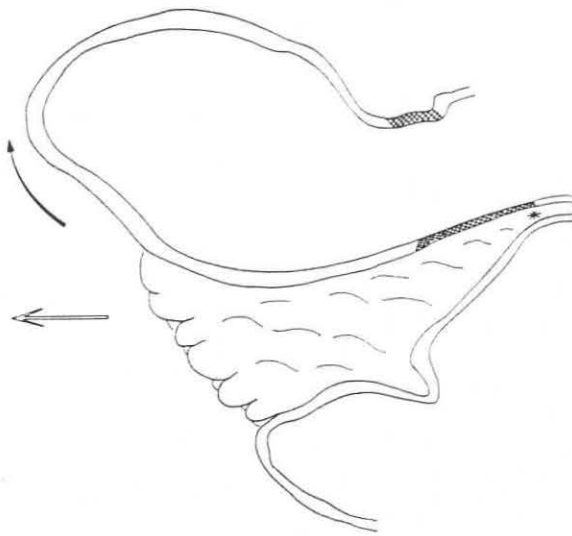
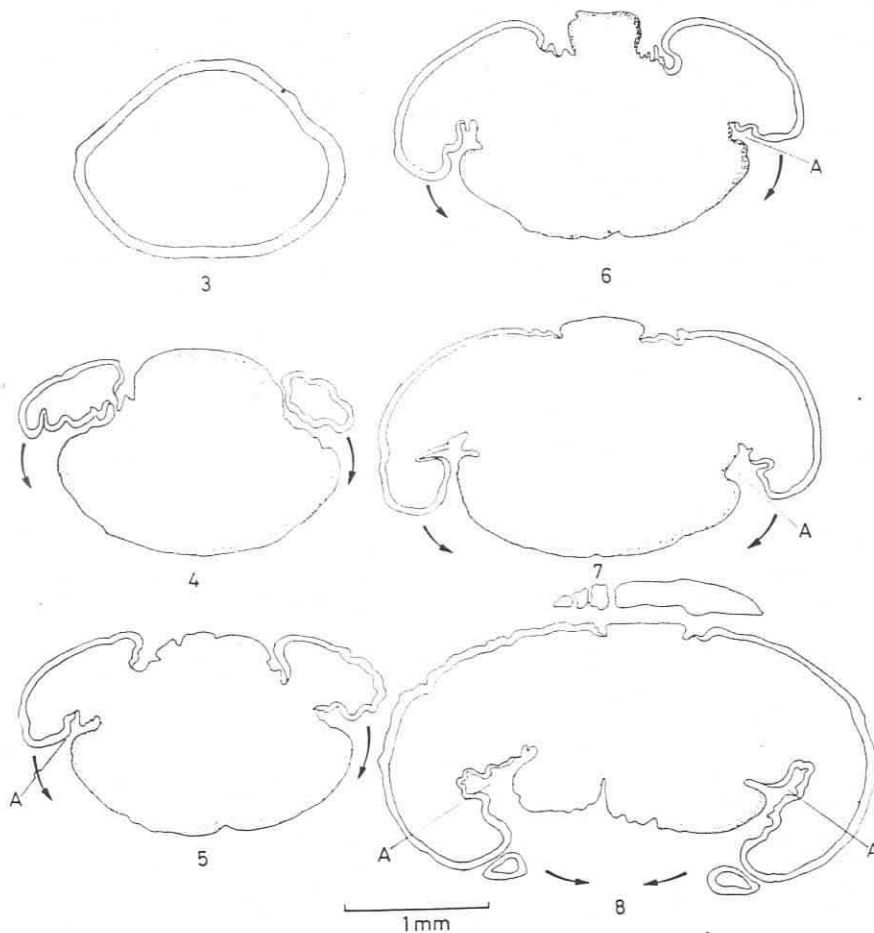


Figure 7.2b. Outline of median sagittal section of the anterior end of *Lumbricus terrestris* with the prostomium protracted to show straightening of fold at its base

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The outline of the prostomium becomes broadly pyriform at some 100 μ from its tip, and the narrowed dorsolateral surfaces are overlapped by forward extensions of the corresponding surfaces of the peristomium, as shown in *Figure 7.4*. On proceeding backwards these peristomial extensions fuse with the



Figures 7.3-7.8. Outline sections to show the relationship between the prostomium (with stippled margins) and the forward extension of the peristomium to form ventrolateral grooves

prostomium dorsolaterally (*Figures 7.5-7.8*) and become increasingly longer in a posteroventral direction, thereby leaving a space between the prostomium and the peristomial folds. Ultimately these folds coalesce mid-ventrally to complete the annular form of the peristomium (*Figure 7.9*). This has been considered to be the 'mouth' by previous workers, and it opens into a space which is bounded laterally and ventrally by the peristomial walls and dorsally by the ventral surface of the prostomium. This space in earlier interpretations has been referred to as the beginnings at least of the buccal cavity and the invagination

(X in Figure 7.2a) at the base of the prostomium as its 'dorsal diverticulum'. To attempt to define precisely what is meant by the mouth—possibly whimsical pedantry—in the sense of its being the functional oral aperture is difficult, for in itself it is merely a space which opens into a cavity—the tube-like gut. But its actual location can only be determined in relation to the structures which

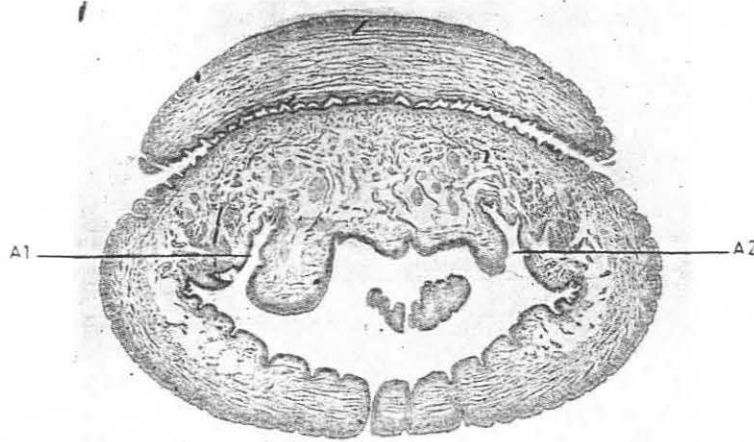


Figure 7.9. Photomicrograph to show coalescence of the peristomial folds to form the entrance of the preoral food cavity

succeed it. In generalized insects, for example, the mouth parts are closely assembled in their attachment on the head, but their components are separated from one another distally so that the space they enclose is in effect a part of the 'outer' world, and is not a cavity *in sensu stricto*. This external space in insects is bounded anteriorly or dorsally (according as to whether the insect is hypognathous or prognathous) by the epipharyngeal wall of the labrum and clypeus, posteriorly or ventrally by the labium and laterally by the mandibles and maxillae. This enclosed space has often been referred to as the 'mouth cavity', and functionally merits this name, but as this region lies outside the oral aperture it is more appropriately called the preoral cavity. The functional oral orifice can only be said to exist when morphological union of these mouth parts has been attained and behind which is to be found a tubular cavity in the form of the gut.

The space between the downfolds of the peristomium and of the prostomium in the earthworm prior to coalescence is obviously 'external' to the earthworm. Examination of isolated transverse sections (e.g. Figure 7.9) in the region of fusion of the peristomial downfolds may, however, give the impression that the space enclosed laterally and ventrally by the peristomial walls and dorsally by the prostomial walls is cut off from the external world. But in fact the spaces marked A₁ and A₂ in Figure 7.9 are continuous with those of A, A in Figures 7.5–7.8. The completed integration of the prostomium and peristomium in the earthworm is effected by the merging of the posterior ventral extremity of the

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prostomium with the fold at its base. The prostomium has been drawn in a retracted position in *Figure 7.2a* and in view of the paucity of circular muscle it seems reasonable to believe that any great degree of protraction will be determined by the thrust from behind. This is maximal when the anterior end is

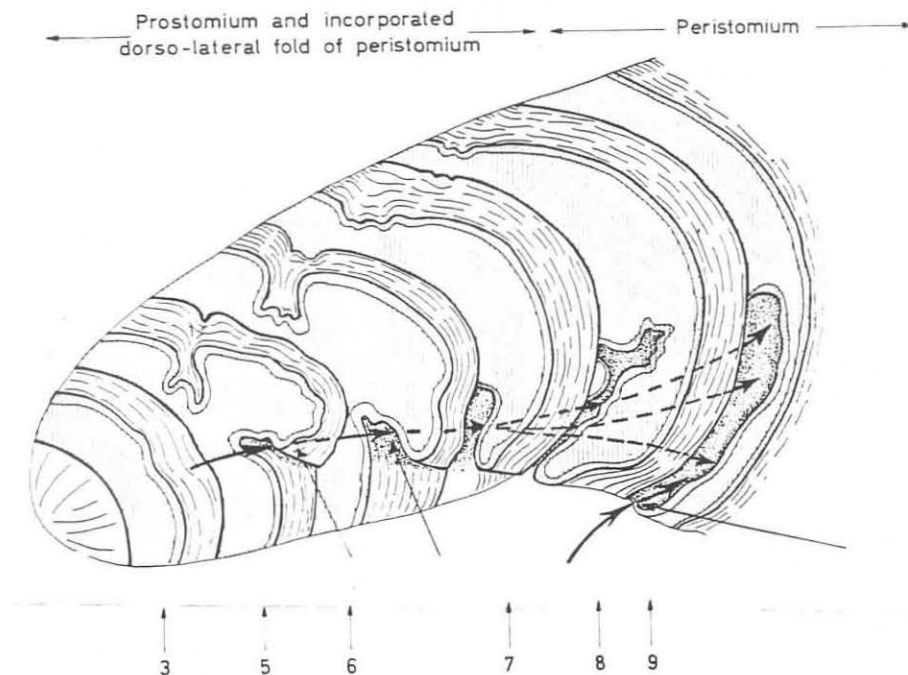


Figure 7.10. Diagrammatic representation to show the relationship of the peristomial folds to the prostomium and to the entrance of the preoral food cavity. In this figure sections (vertical stripes) alternate with the solid body as indicated by short broken lines. The heavy arrows indicate possible routes for entry of soil into the preoral food cavity. The numbered arrows refer to the sections depicted in *Figures 7.3, 7.5, 7.6, 7.7, 7.8 and 7.9*

elongating and will be equal to the total force applied by the coelomic fluid to the first septum, i.e. between segments 4 and 5, because segments 1-4 virtually behave as a solid muscular organ due to the almost complete occlusion of their coelomic cavities. Under such conditions the invagination at the base of the prostomium 'unfolds' (*Figure 7.2b*) and protraction of the prostomium is effected.

The lower or posterior extension of this invagination continues ventrally for a short distance before contributing to the upper wall of the food tract. The lower wall of the latter is formed by the muscular tongue-like outgrowth which morphologically is a lobe of the ventral wall of the second segment. Accordingly we consider that the functional oral aperture lies above this outgrowth and below the fold at the posteroventral base of the prostomium. If this interpretation is correct, then the space lying anterior to this opening is more appropriately considered as the preoral food canal and what has hitherto been

referred to as the 'mouth' should now be regarded as the 'entrance to the preoral food canal'.

This view is not inconsistent with the organization seen in generalized insects and indeed presents a striking analogy, even down to the hypopharynx. This structure in insects extends into the preoral cavity, much as does the 'tongue'-like fold of the earthworm, and the similarity is enhanced in that both structures are morphologically derivatives of the ventral wall.

It is of interest to note that the ventral surface of the prostomium is longitudinally grooved along the mid-line, the groove varying in depth according to the degree of its protraction or retraction. Its function is referred to later.

The buccal cavity and the pharynx. The buccal cavity extends backwards from the oral aperture to just beyond the level of the suprapharyngeal ganglia, where it merges with the pharynx. These two regions are, however, readily distinguishable by their musculature; the pharynx being activated by strong, closely aggregated dilator muscles and characterized by ciliated epithelial walls which are absent from the buccal cavity.

The walls of the buccal cavity consist of an abundance of low, broad folds and irregular plications of varying sizes, and within its lumen the tongue-like process is seen to consist of muscular fibres and loose connective tissue. On passing backwards the tongue becomes broader and deeper, and ultimately fuses with the lateral margins of the cavity. Here, too, the loosely arranged fibres within the tongue condense proximally to form an arc of muscle fibres (*Figures 7.12-7.18*). Fusion of the base of the tongue with the lateral walls of the cavity results in the separation of the buccal cavity from a lower, blind-ending, short, ventral diverticulum, whose walls are somewhat irregularly folded (*Figure 7.13*). The lumen of the buccal chamber above the tongue is bounded by broad, closely set folds, and its surface area is frequently increased by an extensive intucking of the dorsal wall. More posteriorly this infolded region becomes less deep and the epithelial folds bordering the irregular lumen then become deeper and narrower. Below the buccal cavity the band of muscle, already noted at the base of the tongue, now becomes thicker, though retaining its arc-like shape. More peripherally its constituent fibres separate and either pass between the longitudinal muscle blocks to become continuous with the circular muscles of the body wall, or contribute to an ill-defined circular band internal to the longitudinal muscles (*Figures 7.17-7.20*).

At the level of the suprapharyngeal ganglia, and between them and the more ventrally placed buccal cavity, is the anterior limit of a dorsal diverticulum from the pharynx (*Figures 7.21, 7.22*). This diverticulum continues posteriorly for a short distance behind the ganglia where it also broadens and the epithelium becomes deeply folded. Prior to entering the pharynx the mid-region of the roof dips down strongly, whereby the lumen of the diverticulum comes to lie on either side of it. And at about the same level the floor of the pharyngeal diverticulum becomes closely apposed to the roof of the buccal cavity before ultimately coalescing to form a common channel, the pharynx (*Figures 7.22-7.24*).

Dilator muscles arise from the dorsal surface of the diverticulum and form an integral constituent of the downgrowth from its roof. In the first fifth of the pharynx this downgrowth of the roof becomes deeper and broader, the

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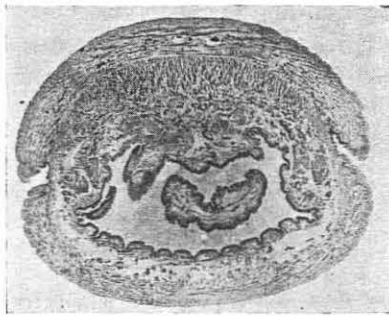


Figure 7.11.

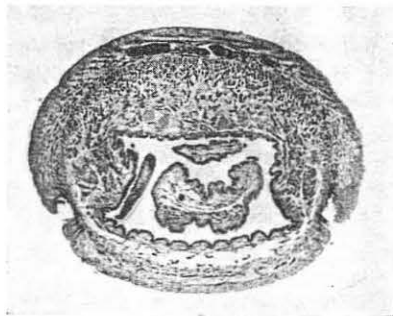


Figure 7.12.

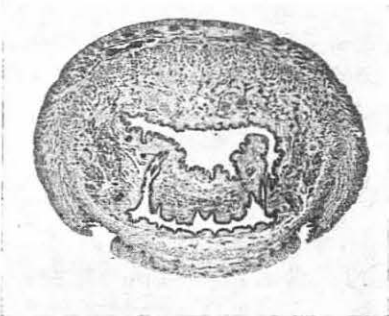


Figure 7.13.



Figure 7.14.



Figure 7.15.

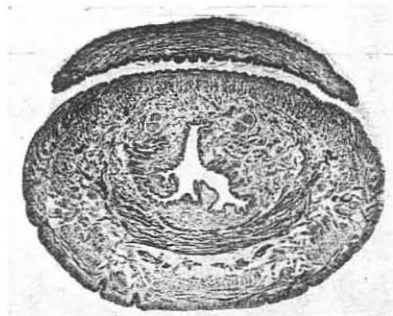


Figure 7.16.

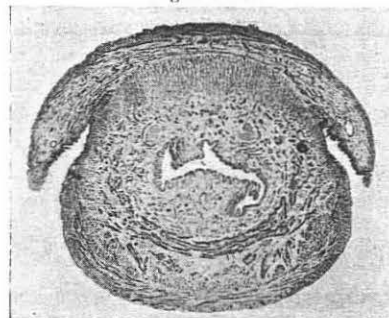


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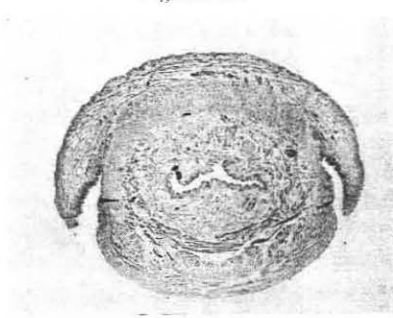


Figure 7.18.

Figures 7.11-7.20 (above and opposite). Selected transverse sections through the buccal cavity to show the relationship between the components. For explanation see text

pharyngeal lumen being narrow and roughly crescent-shaped, although there is considerable branching of the channel at the lateral extremities (*Figure 7.25*). At about the mid-length of the pharynx the lateral curvatures of the lumen become flattened out so that the main axis becomes transverse, and from it arise long branches which insinuate themselves into the dense mass of the overlying pharyngeal muscles and glands (*Figures 7.26–7.28*). More posteriorly the branches shorten, eventually disappearing when the lumen becomes oval in cross section, and into it the oesophagus is introverted. The posterior extremity is provided with a sphincter muscle and in worms, dissected in saline and from which the oesophagus has been removed, its expansion and contraction are readily seen.



Figure 7.19.



Figure 7.20.

The buccal cavity and the pharynx are lined with cuticle, continuous with that of the body wall, and therefore presumably of a collagenous nature. There are, however, isolated patches which lack a cuticular covering in the buccal cavity and these are supplied with ovoid sensory papillae. Such isolated areas and papillae are lacking from the pharynx and in this respect *Lumbricus terrestris* and *Eisenia foetida* agree. The epithelium of the pharyngeal diverticulum, of the dorsal wall, and of the smooth surfaced ventral walls (i.e. apart from the furrowed wall at the entrance) of the pharynx are ciliated and associated with these cells are mucus-secreting cells. The cilia on the dorsal surface are generally longer than those on the ventral surface.

The characteristic structure associated with the pharynx is the extensive musculature and by far the greatest bulk of it is located dorsally where it appears as a lobed mass when seen in dissection from the dorsal side. This muscular arrangement is confirmed from transverse sections. From dissections and serial sections it is noted that the muscles are attached to the septa posteriorly, as bands which pass through the septa to be attached to the body wall in segments 4, 5 and 6 and to the upper surface of the body wall.

The operative mechanisms of the buccal cavity and the pharynx. The food of worms is apparently derived from two sources, viz. the soil, and the surface vegetation which is drawn into their burrows. According to Darwin in his book on 'The formation of vegetable mould through the action of worms', the 'worms always endeavoured to drag the leaves towards their burrows and they tore or sucked off small fragments, whenever the leaves were sufficiently tender. They

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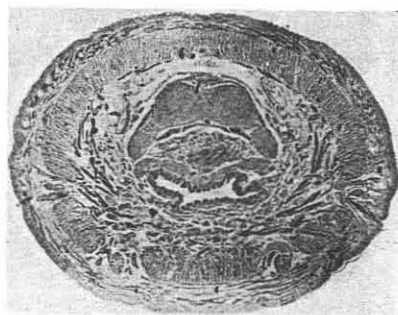


Figure 7.21.

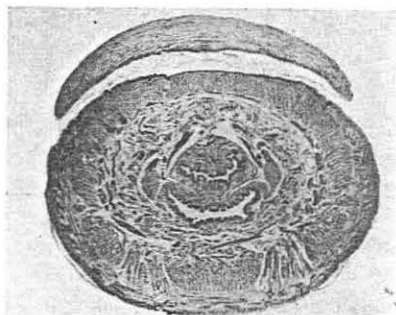


Figure 7.22.

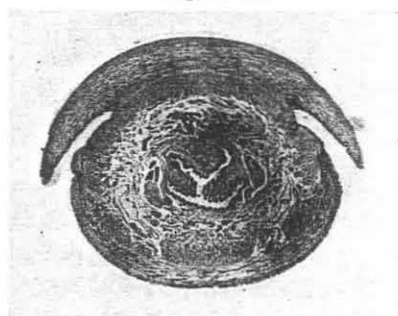


Figure 7.23.

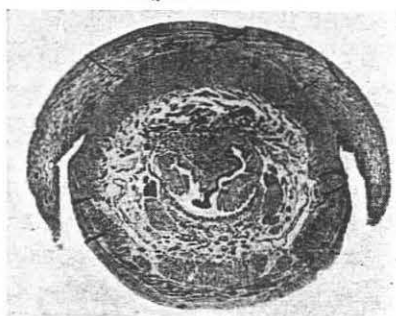


Figure 7.24.

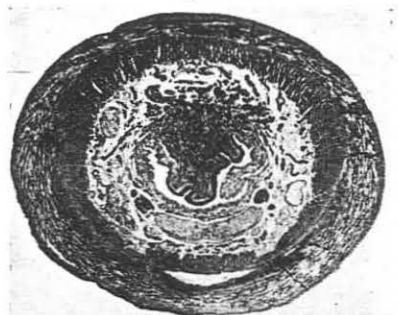


Figure 7.25.

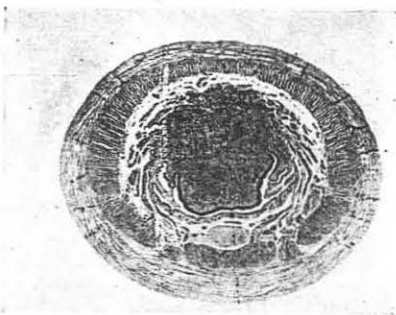


Figure 7.26.

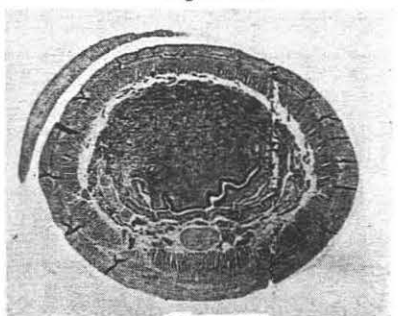


Figure 7.27.

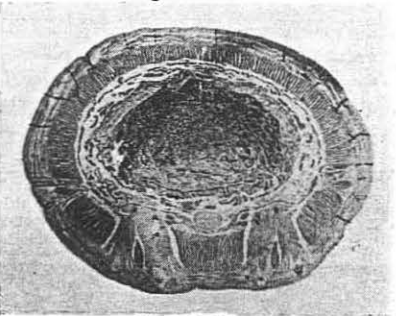


Figure 7.28.

Figures 7.21-7.28. Selected transverse sections through the pharyngeal region to show the relationship between the components. For explanation see text

generally seized the thin edge of a leaf with their mouth, between the projecting upper and lower lip; the thick and strong pharynx being at the same time pushed forwards, within their bodies, so as to afford a point of resistance for the upper lip. In the case of broad flat objects they acted in a wholly different manner. The pointed anterior extremity of the body, after being brought into contact with an object of this kind, was drawn within the adjoining rings, so that it appeared truncated and became as thick as the rest of the body. This part could then be seen to swell a little and this, I believe, is due to the pharynx being pushed a little forwards. Then by a slight withdrawal of the pharynx or by its expansion, a vacuum was produced beneath the truncated slimy end of the body whilst in contact with the object, and by this means the two adhered together'. The excellence of Darwin's detailed observations leaves little room for doubt on the action involved in the intake of leaves into the burrow and it is suggested that a certain amount of extra-oral digestion takes place.

Darwin also put forward the view that an earthworm swallows soil in order to penetrate into the soil, but not necessarily to obtain nutriment, although he comments that 'worms swallow a larger quantity of earth for the sake of extracting any nutritious matter which it may contain than for making their burrows, appears to be certain'. More recently it has been suggested that the soil is ingested while eating food stuffs or during burrow formation through soil too hard for the particles to be pushed aside, and such statements as 'the worm literally eats its way through the soil' are of frequent occurrence in the literature. Even so, the actual process by which soil is taken into the mouth has not been adequately explored.

In a burrowing worm the following phases can be recognized: (a) the attenuation of the first few segments to produce the necessary thrust through the soil, (b) on completion of the thrust the anterior end of the worm begins to expand to be followed by (c) the attainment of maximum thickness, and (d) the further attenuation of the anterior end preparatory to a new thrust. Presumably, too, there must be periods when the worm is in a resting condition and at such times both sets of muscles are in a 'holding' state i.e. neither minimally nor maximally contracted.

The possibilities as to the time and manner in which soil can be ingested might now be considered in relation to the above data. During the phase of segmental attenuation the body circular muscles are contracted and this would apply equally to those of the circular muscles on the 'lower' lip (=ventral part of peristomium) at the opening of the preoral food canal. This gape would then tend to be closed and it appears unlikely that the ventral region of the peristomium will act as an efficient scoop. One other feature needs comment here. The peristomial folds are supplied with incomplete bands of peripheral 'circular' muscles, whose fibres run vertically relative to the longitudinal axis. On contraction, which they do in unison with the circular bands of the peristomium, they pull the fold upward and outward. This is possible only by virtue of (a) the disposition of these muscles and of (b) the much folded cuticle in the angle between the peristomial fold and the more solid mesial structures (Figures 7.5-7.8). The net result of this movement is to increase the width of the groove, and since the adjacent segments are also in a state of attenuation the worm can be actively progressing through the soil. During such progression particulate matter can be collected passively in these grooves, and since these

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converge to form the mouth, it may well be one of the ways in which soil passes to the vicinity of the preoral food canal (*Figure 7.10*). Closure of the grooves is effected by the contraction of the dorso-ventral system of muscles and the relaxation of the incomplete circular bands, with the folds in the angle becoming prominent once more. In other words, the fulcrum for movement lies in this angle.

Cinephotographs of burrowing worms show that the protracted prostomium can be flexed upwards, whereby the preoral cavity is brought into intimate contact with the external medium. This is diagrammatically illustrated in *Figure 7.2b*, and is mechanically possible because the ventral fold at the base of the prostomium is longer than that on the dorsal and dorsolateral faces. We have noted that the ventral surface of the prostomium is grooved, and it becomes deeper on contraction of the oblique longitudinal muscles, which are responsible for its depression and retraction. Thus it is conceivable that during this action the prostomium will act as a downward scoop bringing soil particles with it into the preoral canal and to the vicinity of the oral aperture.

Speculatively it is suggested that during attenuation of the segments the buccal cavity is occluded because it lacks a heavy intrinsic musculature to oppose the circular muscles of the body wall, but as we have noted there is a possibility of aggregation of soil in the vicinity of the preoral food opening. Thus the actual soil intake into the preoral aperture occurs when the segments are in a stage of transition between attenuation and thickening, i.e. when the pressures on the wall of the buccal cavity are being released with the consequent establishment of a partial vacuum and the soil sucked in. That the pharynx can exert a further suction has already been recognized and by this means the soil will pass from the buccal cavity to the pharynx.

Recent workers¹⁹ have reported the eversion of the pharynx (although we believe this to be the lining of the buccal cavity) through the preoral food opening, and have suggested that it acts as a taste organ, for its protrusion often precedes a change of direction in burrowing. Some standard texts continue to report that the pharynx of oligochaetes is not eversible, although it is unquestionable that 'structures of one sort or another' are everted through the preoral food entrance. From preparations it is also evident that the tissues so forced out do not involve the lining of the preoral food canal. Ligaturing of the folds when extended to their maximum also confirms the opinion that it is the lining of the buccal cavity which is everted and that the pharynx remains in its original position. As already noted, the lining tissues of the buccal cavity are much folded and that posterior to, and incorporated into the proximal region of the tongue is a broad arcuate band of sub-buccal muscles. Contraction of this muscle, simultaneously with that of the body circular muscles, exerts pressure on the bounding layer around the lumen by way of the intervening connective tissue. The presence of a firm dorsoventrally flattened pharyngeal lumen posterior to the buccal cavity prevents backward extension of the folds of the buccal epithelium into it, and this together with the unfolding of the invagination of the base of the prostomium will cause the buccal cavity to be extruded anteriorly through the oral aperture. By this means the maximum surface area of the lining of the buccal cavity bearing the olfactory sensory areas is exposed to the influences of the environment. This sensory area is innervated by nerves originating in a pair of ganglia on the mesial side of the commissures, and which

form a dense plexus lying both dorsal and ventral to the buccal cavity and in front of the suprapharyngeal ganglia (*Figure 7.21*). Extrusion of the buccal epithelium on to a glass slide shows that copious quantities of mucus are passed out and to this soil particles adhere, which on retraction of the buccal lining are then taken into the oral aperture.

No intrinsic muscular system appears to be present to cause eversion of the pharynx, though this doubtless could be effected by increased pressures developed by the body musculature, but there is no evidence to support it. Direct observation and cine photographs show the structures remain everted irrespective of cycles of extension and contraction of the segments. Moreover, it is questionable whether the mass of the dorsal pharyngeal muscles, even in a highly relaxed state, could be forced out between the suprapharyngeal-commissures-subpharyngeal ganglia complex.

It is unlikely that soil can be drawn into the mouth when the anterior segments are at their thickest because of the very considerable telescoping of these segments, including the prostomium, whereby the gape to the preoral food canal is completely occluded. In fact, it is only by the close vice-like apposition of the lower surface of the prostomium and the inner surface of the peristomium that, as described by Darwin, 'vegetable material can be held prior to dragging it from the surface into its burrow'. There would seem to be no inherent difficulty in the 'resting' worm sucking in soil, for the gape of the preoral canal would be in an open position and independent movements of the pharyngeal muscles would be possible, so producing the necessary suction for intake of soil and nutrient material. But the pharynx also functions as a force pump whose action reinforces that of peristalsis of the oesophagus (see later) and propels food down as far as the gizzard. Mechanically this is only possible by having (a) an occluser mechanism to prevent backflow of contents from the oesophagus during the ingesting phase and (b) a device to prevent regurgitation from the pharynx to the buccal cavity during the propulsive phase. The presence of a sphincter muscle to cope with (a) has already been noted. Movements of ingested material along the pharynx are possible either by anteroposterior peristaltic waves or by the occlusion of the lumen anteriorly if pharyngeal action is non-peristaltic. The first method presupposes that there is an adequate circular musculature circumventing the pharynx to work antagonistically against the dilators but such muscles are singularly lacking. The second requires that the walls have an intrinsic elasticity possibly due to the cuticular lining and an anteriorly placed 'valvular' apparatus so that the lumen could be occluded. As far as can be ascertained this need is met by the crescent-shaped downgrowth from the roof of the anterior part of the pharynx fitting closely against its floor (*Figure 7.26*).

Pharyngeal glands. Stained sections through the pharyngeal mass reveal deeply staining cellular components in the dorsal and lateral portions of the mass, but they also extend more deeply into the mass between the muscle bands. Here they are fewer in number and in general the cells are smaller in size. The cells assume a variety of shapes and are frequently widely separated

from one another. The cell body stains deeply in part and the nucleus, which often contains a visible nucleolus, may be obscured by the more deeply staining cytoplasm. A capsule of flattened cells covers the mass, but incompletely; sometimes it is continuous in places with the underlying gland cells, and in places is absent altogether. The secretions from the glandular cells pass between the muscle fibres and penetrate into the deeper part of the pharyngeal mass whence, in *Aulophorus* and *Eisenia foetida*, they flow between the epithelial cells bounding the pharyngeal lumen and enter into the lumen. 'Mucin' ducts are alleged to occur in a *Lumbricus* sp and *Allolobophora* sp. The secretion from the glands of *Lumbricus* also contains a proteolytic enzyme and more recently a detailed analysis of secretions in *E. foetida* has shown them to contain an acid mucopolysaccharide and an amylase, but probably no proteolytic enzyme. The optimum for this activity occurs at pH 6.5. Doubtless the secreted mucin serves to lubricate the food.

The lumen of the pharynx opens into the antero-dorsal part of the oesophagus, part of which extends forwards beneath the pharynx as a closed pocket or diverticulum. The oesophagus extends, behind its junction with the pharynx, from about segment 6 to segment 14, and is folded transversely when seen *in situ* and undifferentiated externally. When opened longitudinally the following regions are distinguishable:

(a) A long anterior section extends from the pharynx to the level of the openings of the oesophageal pouches on its lateroventral walls. The columnar epithelium of this section is thrown into folds which are separated by deep, narrow grooves (*Figure 7.32*). The alternate flattening and raising of these folds and of the folding and unfolding of the tract brings about movement of food and soil along it. This is effected by the inner layer of circular muscles and the outer layer of longitudinal muscles, both of which are surrounded by the peritoneal epithelium and a layer of chloragogenous cells.

For the greater part of its length this region is circular in cross section, but near its junction with the middle section and slightly in front of the opening of the pouches into the oesophagus it becomes flattened from side to side and the endothelial folds, characteristic of the anterior part of the oesophagus, are retained (*Figure 7.33*). These folds cease at the level of the opening of the pouches, except in the dorsal and ventral regions (*Figure 7.34*).

(b) The middle part of the oesophagus is relatively short and into it open the pair of oesophageal pouches in segment 10. Two pairs of oesophageal glands in segments 11 and 12 are evident as dilatations of the oesophageal wall.

The openings of the pouches onto the anteroventral walls of the oesophagus are guarded by broad, backwardly directed, highly vascularized flaps. Sphincter muscles in the necks of the pouches allow the entrances to the oesophagus to be periodically opened and closed. The pouches, which are forwardly directed *cul-de-sac* like extensions of the oesophagus, have a well defined epithelium around the lumen, and between it and the muscular layers are interposed a series of interlamellar spaces separated by radial lamellae. These spaces open between folds of the pouch wall. Beneath the circular

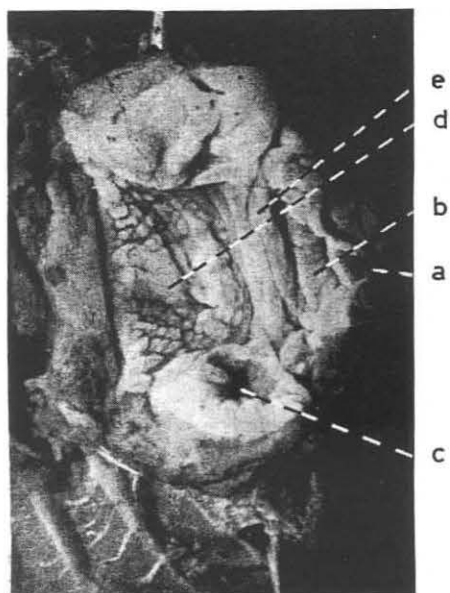


Figure 7.29. Dissection of the pharynx and buccal cavity to show a, entrance to preoral food channel; b, 'tongue' like fold; c, openings of pharyngeal diverticula; d, the pharynx; e, the buccal cavity

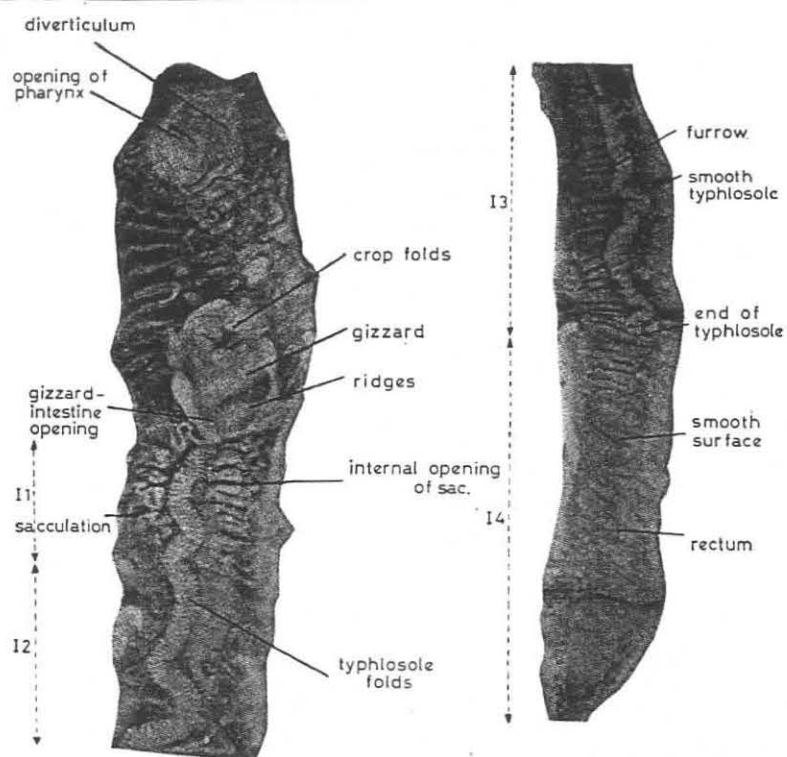


Figure 7.30. Dissection of *L. terrestris* showing the crop, gizzard and anterior part of intestine opened up longitudinally on the ventral surface
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Figure 7.31. Dissection of *L. terrestris* from the ventral side to show the smooth part of the typhlosol and the hind intestine from which the typhlosol is absent
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muscles of the walls and adjacent to the epithelium are blood sinuses, which are connected to each other by vessels running radially within the substance of the lamellae. In worms dissected under saline the outer blood sinuses appear as longitudinal red tracts when they are in diastole, but become almost colourless during systole.

Posterior to the opening of the pouches the lumen of the oesophagus is long, narrow and dorsoventrally orientated (*Figures 7.35-7.37*), with the lateral walls generally flattened and the dorsal and ventral regions folded. This shape persists to just in front of the posterior limit of the second pair of glands, but more posteriorly the lateral walls become abundantly grooved (*Figure 7.38*). The grooves deepen towards the crop and beyond the hind margin of the second pair of glands the laterally flattened oesophagus gradually assumes a rounded outline in transverse section (*Figure 7.39*). The epithelium of the lateral faces is ciliated, except for the folded dorsal and ventral regions. The cilia are evident in sections, and can be demonstrated by opening up the oesophagus under saline. Microcrystalline spherules of calcium carbonate passed out from the pouches, together with particulate matter in the tract, are caught up in mucus strings and wafted by the cilia in the direction of the crop at a not inconsiderable speed. Radial lamellae, and their associated inter-lamellar spaces, between the oesophageal epithelium bounding the lumen and its circular muscles, are characteristic of this section. These horizontal lamellae are continuous in a longitudinal plane with those of the pouches. Thus we have the formation of a series of longitudinal inter-lamellar spaces along which material can pass from the channels in the oesophageal wall directly into those of the pouch.

The oesophageal glands, like the pouches, are specializations of the oesophageal epithelium. Each gland is made up of a series of lamellae covered with epithelia whose small finger-like processes protrude into the inter-lamellar cavities.

The first pair of glands are free of the oesophagus anteriorly while further back their mesial surfaces become closely apposed to the outer walls of the oesophagus. These walls eventually fuse completely and produce the forms depicted in *Figures 7.36, 7.37*. By this union the inter-lamellar spaces of the glands communicate directly with those within the oesophageal wall in a radial direction as a result of the fusion of the lamellae of the oesophagus and of the gland. The lamellae of the oesophagus lack the finger-like processes of those of the glands. Microcrystalline spherules of calcium carbonate, secreted by the cytoplasm of the gland epithelium, will thus follow a radial course from the inter-lamellar spaces of the gland to those of the oesophagus, thence longitudinally into the inter-lamellar spaces of the pouches. The path of such spherules can readily be observed in worms dissected under saline under high magnification of the binocular microscope. Most of the British genera possess both glands and pouches, although the latter are lacking in *Eisenia* sp. and *Helodrilus* sp. Recently it has been shown in *Eisenia foetida* that the cellular biochemical mechanisms involved in the elimination of calcium from the

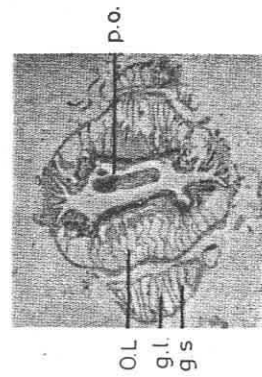


Figure 7.32



Figure 7.33

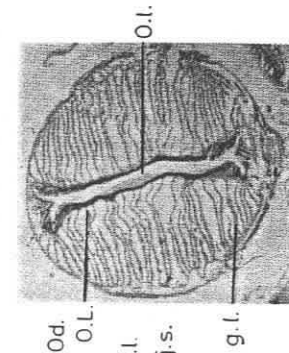


Figure 7.34

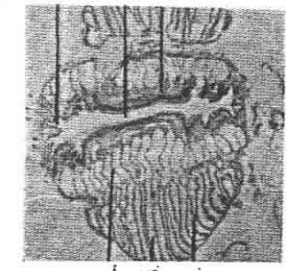


Figure 7.35

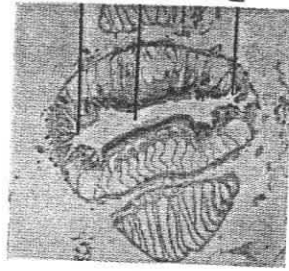


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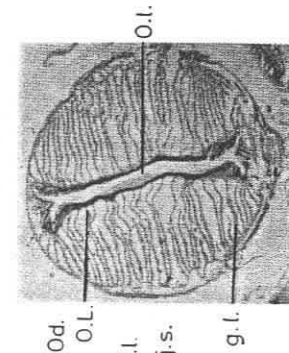


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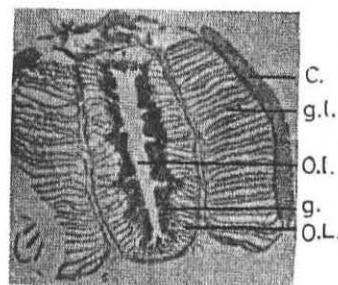


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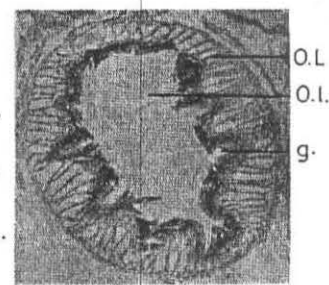


Figure 7.39

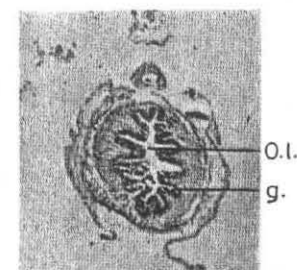


Figure 7.40

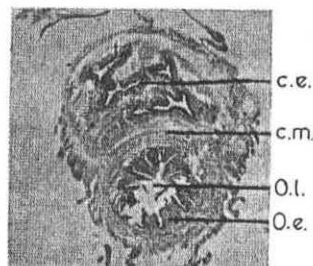


Figure 7.41



Figure 7.42

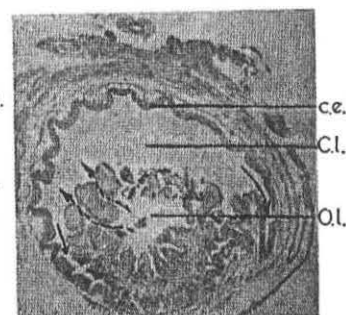


Figure 7.43

Figures 7.32–7.43. Transverse sections through the oesophagus (32–40) and the junction of the oesophagus and crop (41–43). For explanation see text

O.e., oesophageal epithelium; l, lumen of pouch; lm, lamella of pouch; i.s., interlamellar space; O.l., oesophageal lumen; O.L., oesophageal lamella; p.o., opening of pouch into oesophagus; g.l., gland lamella; g.s., gland space; F.Od., dorsal folds of oesophagus; F.Ov., ventral folds of oesophagus; C, chloragogenous cells; g, grooves of oesophagus; c.e., crop epithelium; c.m., circular muscles; b, muscle strands; C.l., crop lumen; l.j.s., internal sinus

Broken arrows in Figure 7.43 show connections between oesophagus and crop; solid arrows show downward extension of crop lumen

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anterior and posterior parts of the glands may differ (van Gansen²⁰). The secretory cells of the posterior portion contain rod-like structures, or 'bâtonnets', and several types of mitochondria, but with no inclusions of microcrystalline calcium carbonate. The 'bâtonnets' have been interpreted as the cytomembranes of the cells and adjacent to the glandular lumen these cells are ciliated and bear outgrowths reminiscent of a brush border. The more anterior parts of the gland lack the 'bâtonnets' and have an abundance of calcium carbonate concretions. In common with many organs which have high metabolic rates and are associated with secretory, or absorptive functions, the calciferous glands are well supplied with alkaline phosphatase. The posterior section receives a blood supply directly from the intestine and the fluid content of the cells is almost identical with blood, so that by a process of active filtration the high molecular organic compounds are retained within the blood. Meanwhile, the fluid contents of the interior of the glands are concentrated by absorption of certain salts and water until the calcium carbonate precipitates out in the lumen of the gland without ever being in solid form in the cells of the gland. The occurrence in the anterior region of microcrystalline deposits in the cells is suggestive of an alteration of the blood constituents and that the aggregations form as a consequence, to be released by the rupture of the cells into the lumen.

In *Eisenia foetida* the microcrystalline secretions are passed into the oesophagus by way of a series of small pores from the anterior part of the gland. Whereas in worms possessing pouches in addition to glands a proportion of the microcrystalline secretions of the latter are transformed to crystals of calcite; some of the calcium carbonate is excreted in the form of granules. The passage of the granules along the tract is facilitated by being bound up with mucoid secretions and wafted along by cilia to the crop. In this structure there is considerable admixture of the spherules with the soil. Now since there is no difference in the physical state of the crop contents and the gizzard contents it is tentatively suggested that the calcium in the microcrystalline form may assist flocculation of soil in the crop where, as will be seen later, there is considerable agitation of the soil.

The ingestion of soil and vegetation often entails the intake of associated acid soil particles and organic acids and it was at one time thought that the calcium carbonate secreted by the calciferous glands neutralized the acidity of such compounds. The recovery of calcium carbonate concretions in worm casts from very acid media, and the observation that pH values of such casts approximate to those of ingested soil do not lend credence to this view. Large earthworms appear to be abundant in calcareous localities and, doubtless, calcium in some form is ingested, and the suggestion has been made from time to time that the glands excrete excess calcium carbonate. Direct evidence of the absorption of this compound in the gut is lacking, and calcite crystals do not dissociate at the pH (6.4-7.0) prevailing in the gut. It is now realized that they exercise no reaction on the gut contents and that the cause of such neutralization are the secretions of the intestine as a whole. The blood supply to the

glands comes from the dorsal vessel, into which open segmental vessels from the intestine as well as vessels from the chloragogen cells. If calcium is absorbed from either of these sources the calcium glands are well placed to remove excessive quantities from either and to pass the concretions of calcium carbonate into the lumen of the oesophagus. They will then traverse the length of the gut, and analysis of casts egested at the anus suggests most strongly that calcium carbonate is not absorbed²⁵. Since *L. terrestris* is known to feed on leaves, one of the sources of calcium for earthworms would appear to be putrescent plant material. The sparingly soluble calcium oxalate, which occurs in crystalline form in plant cells, may be one such source. The crystals may be single, including raphides, which are abundant in Monocotyledons, or druses, which are spheroidal groups of tetragonal crystals built around an organic core, as in rhubarb, or as crystal-sand masses of microspheroidal crystals packed into a cell. The cell sap of plants also contains free calcium ions, whilst the putrefaction of plant tissues results in the breakdown of calcium pectate of the cell wall and the subsequent release of calcium. But in whatever form calcium is absorbed by the gut, it must be soluble and diffusible. Alternatively, calcium can be ingested in its absorbable form as calcium nitrate, which is occasionally found in the soil as a product of the action of nitrifying bacteria.

For the next paragraph or so we will digress a little in order to understand the possible role of the glands in respiratory exchange. Animals which are truly terrestrial, i.e. live on the surface of soil, can count upon 21 per cent of oxygen being available in the atmosphere for respiratory purposes, and the normal concentration of atmospheric carbon dioxide is 0.03 per cent. Lumbricid worms, however, live *on* the surface and *in* the substrate. Thus the carbon dioxide may rise to 0.25 per cent within the soil at a depth of 6 inches, and in wet soils may rise considerably above this for short periods²¹. Flooding of burrows results in the migration of worms from them to the surface. Experiments with *Eisenia foetida* show that at concentrations of 25–100 per cent CO₂ many earthworms take evasive action, whilst at concentrations of 6–12.5 per cent worms progress in their original direction, only being temporarily impeded²². The earthworm is not known to take any special action to renew the air in its burrows, and under flooded conditions the availability of oxygen is much reduced. Now the rate of diffusion of oxygen in water is many thousand times less than its rate of diffusion in air, and oxygen has a low solubility in water. The still water in the burrows remains in contact with the respiratory surfaces of the worm, and the oxygen in layers close by the worm is quickly used up and the rate at which it is renewed by diffusion from more distant layers becomes inadequate to meet the animal's requirements.

If worms are kept for a week or so in calcium nitrate or calcium chloride solutions, from which calcium carbonate is excluded, any carbonate formed at the end of the experiment must be due to the production of carbon dioxide during their metabolism. The results show that the percentage of CO₂ removed as carbonate under these conditions is in the range of 5–10 per cent of the total CO₂ output²³. Equally, by subjecting worms to CO₂ in gaseous atmospheres of

14 per cent CO_2 for 5 days or 25 per cent CO_2 for 3 days, there is a diminution of the concretions in the calcareous glands, which has been interpreted as being due to unsuitable conditions of CO_2 stress, with the subsequent removal of tissue CO_2 as carbonate via the glandular concretions²⁴. Up to a concentration of about 12.5 per cent of atmospheric carbon dioxide no inimical effects are produced on worms, and since they can remove about 10 per cent of the atmospheric carbon dioxide by way of the calciferous glands under stress, the accumulation of CO_2 in the burrows does not adequately explain earthworm migrations under flooded conditions. Accordingly it would seem to be more feasible to believe that this is due to oxygen lack.

Increase in the carbon dioxide concentration in the body of the worm, whether it is derived from outside sources or as a result of metabolic activities of its tissues, could affect the hydrogen ion concentration of the body fluids and thus influence the oxygen dissociation curve of the haemoglobin. But subjecting a worm to 25 per cent CO_2 for 16 hours does not materially affect the pH of the coelomic fluid, which is suggestive of the occurrence of a buffering mechanism²⁵. Extirpation of the calciferous glands prior to treatment with even lower carbon dioxide tensions for shorter periods results in increasing acidity of body fluids due to the accumulation of CO_2 in the tissues. Analysis of tissues of such worms shows there is an increased level of calcium distributed through the body, instead of being bound to carbon dioxide and excreted as carbonate. The available evidence then indicates that the calciferous glands fix a certain percentage of the metabolic carbon dioxide and this can be regulated according to the availability of atmospheric carbon dioxide.

The enzyme carbonic anhydrase, which plays a vital role in CO_2 transport in vertebrate tissues and is involved in the reversible reaction of carbon dioxide and water to produce carbonic acid, also occurs in earthworms. It is present in the calciferous glands, oesophagus, crop and gizzard and quantitatively decreases in this order²⁶. The carbonic anhydrase is associated with systems that cause shifts of pH such as those which occur during the secretion of hydrogen ions.

The oesophagus, posterior to the calciferous glands, is short and round in transverse section. When compared with the middle part of the oesophagus its overall diameter is substantially reduced, the epithelial folds and depressions more accentuated, and the cilia are no longer present (*Figure 7.40*).

Crop. The oesophagus is succeeded by the crop, a dilated thin walled part of the alimentary canal, which it enters ventrally. The anterodorsal part of the crop overlaps the hinder end of the oesophagus and the epithelium of the former is thrown into large irregular folds (*Figures 7.41, 7.42*). On opening up the crop of a living worm under saline the folded, yellow coloured epithelium is forced out through the incision, as if under pressure, and under these conditions and presumably in life it occupies much of the space within this structure. This epithelium exhibits strong dilating, contracting and twisting movements when the crop is opened under saline. The oesophagus continues back ventrally for some distance within the peritoneal layer of the crop where its longitudinal muscles lose their circumferential character, retaining only their ventral portion which becomes integrated with the corresponding musculature of the crop. The circular muscles of the oesophagus retain their original form, and their upper regions are closely apposed to the lower regions of the corresponding

muscles of the crop (Figure 7.41). For a short distance posteriorly the epithelia of the crop and of the oesophagus are separated by these muscles and sub-epithelial connective tissues before they become vacuolate, and finally the epithelia fuse together. These epithelia extend backwards as the irregular folds lining the crop, and they are separated from one another by channels which link the oesophagus with the crop lumen (Figure 7.43).

The backward continuation of the oesophagus into the crop may operate as a device for preventing the regurgitation of the crop contents into the oesophagus during the contraction of the former, whilst the folds and accompanying grooves of the crop epithelium may regulate the speed at which the contents of the crop pass into the gizzard. Such material, caught up in the channels between the folds, follows a wandering course in this 'maze' before being

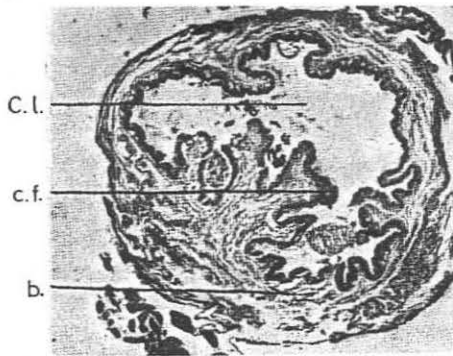


Figure 7.44. Transverse section of entire crop to show folded nature of epithelium with muscular and connective tissue strands. C.l., crop lumen; c.f., crop epithelium; b, bands of muscular tissue

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released into the gizzard. The soil within the crop is generally finer than the form in which it is ingested and possibly this change is enhanced by the movements of the folds. In some annelids, e.g. *Eisenia* or *Helodrilus*, where the calcium carbonate spherules pass from the glands directly into the oesophagus, the fold movements would assist in mixing this secretion with the soil and possibly aid in soil flocculation.

The crop epithelium is separated from the circular band of muscles by discrete connective tissue and muscular strands. The latter originate as fibres from the more compact circular band and are supplemented by longitudinal muscle strands. The epithelial cells are of the columnar type, have a striated border, and are covered with a thin cuticle which is insoluble in caustic potash. The ample supply of crop blood vessels is longitudinally arranged beneath the epithelium, although in some instances the blood vessels may run between the bases of the constituent cells.

The crop contracts more frequently than does the gizzard, and *in situ* undergoes powerful constricting movements which are very much stronger than are those of the gizzard. The entry of the crop into the gizzard is very broad, but sphincter muscles in the wall of the crop can occlude the lumen.

Gizzard. The thick muscular wall of the gizzard is arranged in three bands beneath the thin peritoneal layer. The outer longitudinal muscle band is about

0.01 mm thick, the middle one of radially arranged longitudinal muscle bands about ten times as thick, and the innermost layer of circular muscles of 0.85 mm radial thickness. Between these muscular bands are fibres which give staining reactions suggestive of collagen.

Columnar epithelial cells bound the lumen which in the anterior half are covered by a longitudinally ridged thick layer of cuticle. This cuticle is not stable in hot dilute alkali, does not crystallize and though chitin-like is not in the α -chitin form. Chemical tests with orcein, resorcin, van Giemsa, benzidine and Gomori stain show that it has an affinity with vertebrate elastin. It differs from it, however, in not being birefringent or autofluorescent. Its hydrolysis produces proline, hydroxyproline, valine and glycine. Posteriorly its epithelium is thrown into short thick folds, which are capable of independent movement due to the intrinsic strands of muscle which infiltrate into them. A sphincter muscle, composed almost entirely of circular muscles, controls the passage of food from the gizzard to the tubular intestine which follows.

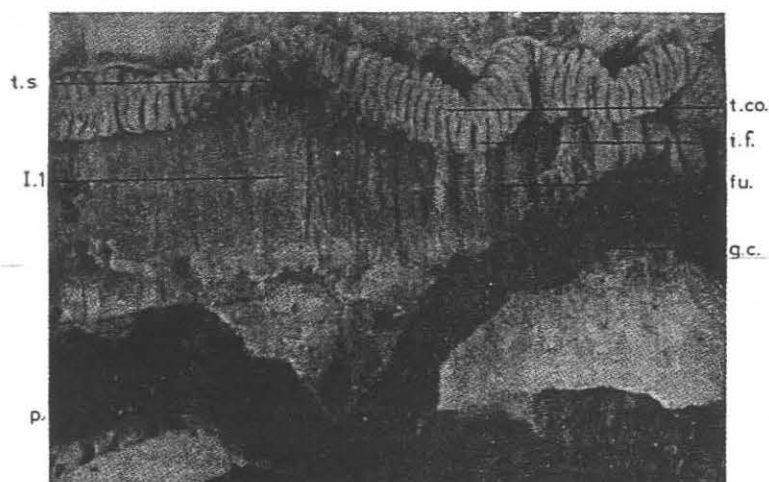


Figure 7.45. Dissection of part of the intestine from the ventral surface in the region of the typhlosolar folds with the gut contents displaced. t.s., epithelium removed to show the 'collagenous' type of tissue; t.co., oblique transverse connection between the typhlosolar folds; i.f., typhlosolar fold; fu., furrow; g.c., gut contents; I.l., intestinal lumen; p., peritrophic membrane

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Intestine. Externally the intestine is clearly divisible into two sections when dissected in saline. A short anterior portion immediately succeeding the gizzard has dorsolateral and ventrolateral sac-like dilatations arising from its walls and *in vivo* these show rhythmic expansions and contractions (Figure 7.30). Nevertheless histologically and histochemically the components of the walls are similar to those of the rest of the gut, although the epithelium is thickened due to increased foldings. The remainder of the intestine is of uniform external appearance and covered with chloragogenous tissue.

Internally the structure is more complex, particularly in respect of the typhlosole. The typhlosolar region occupies about the anterior two-thirds of the intestine, whilst the remaining third lacks a typhlosole. The anterior section of

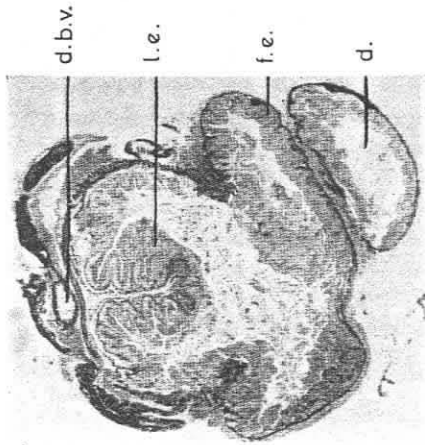


Figure 7.48

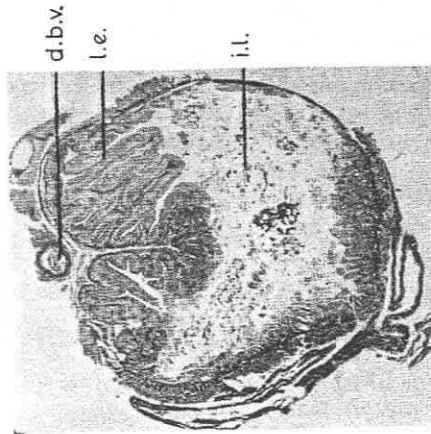


Figure 7.51

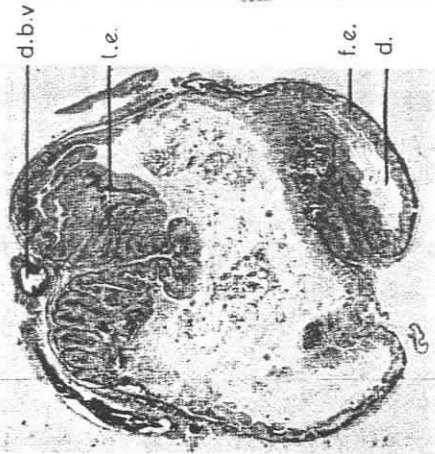


Figure 7.47

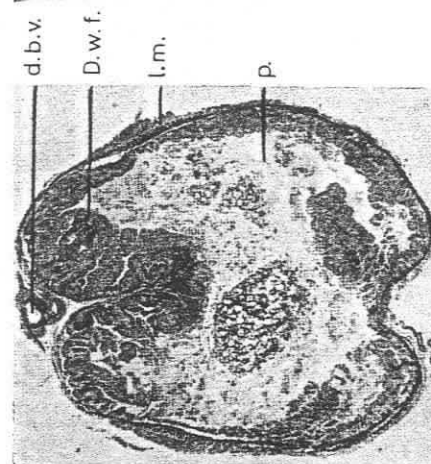


Figure 7.50

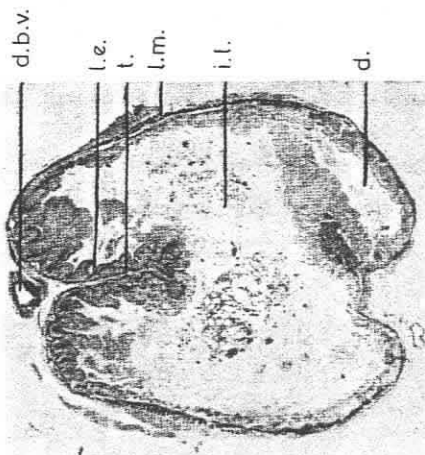


Figure 7.46

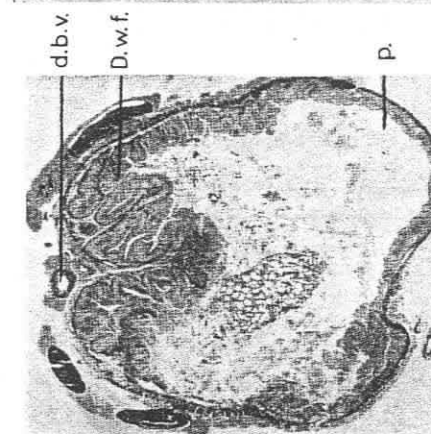


Figure 7.49

Figures 7.46–7.51. Transverse sections through the fore part of the anterior intestine to show the changing form of the typhlosole. d.b.v., dorsal blood vessel; l.e., lateral epithelium; t., typhlosole; l.m., thickened portion of longitudinal muscles; i.l., intestinal lumen; d., sac-like dilatation; f.e., folded epithelium; D.w.f., dorsal wall folds; p., peritrophic membrane. For explanation see text

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the typhlosole consists of a series of transverse folds, separated by deep grooves, which bear no relation to body segmentation (*Figure 7.45*). The folds on either side are united along the midventral line by short connections. The folds in the intestine immediately behind the gizzard are arranged opposite to one another, but more posteriorly those on the right alternate with those on the left.

At the level of the groove separating adjacent folds the epithelium overlying the vertical axis of the typhlosole (=lateral epithelium) is narrow and shows only weak plications, but midventrally is broadly expanded (*Figure 7.46*). Transverse serial sections through a single fold show an increase in these plications towards its midlength and they join up with prominent folds of the dorsolateral wall of the gut (*Figures 7.47-7.49*). Large numbers of mucoid secretory cells occur on the free surface of the typhlosole, but are lacking from the rest of the gut epithelium, which is characterized by columnar ciliated cells and enzyme secretory cells. Most of the latter have reticulate cytoplasm and contain acidophilic zymogen granules enclosed in vacuoles. Shrunken vacuolated cells are present nearer to the basement membrane and they may be enzyme cells undergoing restitution after a period of activity. Their cytoplasm is markedly basophilic and may contain a few secretory granules.

When suitably stimulated with food the cilia of the epithelium cells beat dorsoventrally and concomitantly the glandular cells of the typhlosole secrete a 'mucoid' material. This is wafted downwards over the walls, thereby forming a lining or 'peritrophic membrane' to the epithelial cells. The membrane is thin, lacks the stickiness of mucus, is translucent and tears readily. This membrane gives a positive reaction for acid mucopolysaccharides in *L. terrestris* (*Figure 7.45*). Bearing in mind that the contents of the alimentary canal are changed at least once every 24 hours, the production of this acid mucopolysaccharide membrane during life of the worm must be very considerable. There is a general acceptance of the view that the typhlosole augments the absorptive surface, but to what extent this function is true for all annelids is questionable, e.g. in *Eiseniella tetraedra* it is a simple elevation, in *Megascolex caeruleus* it is a mere ridge, and in the largest of all known earthworms, *Megascolides australis*, it is absent.

As already mentioned, a short region immediately succeeding the gizzard is differentiated to form a sacculated zone whose dilatations open into the lumen of the intestine through long narrow dorsoventrally orientated apertures. This contrasts with the succeeding section where sac-like dilatations are lacking and the internal walls are strongly furrowed (*Figures 7.30, 7.31*). The posterior part of the typhlosole forms a smooth-walled dorsal intucking of the gut wall. The internal surface of the wall of the gut associated with this part of the fold is similar to that of the second part associated with the folded typhlosole. Behind the typhlosolar region the walls lose their furrowed appearance and are relatively smooth, although much folded.

Underlying the epithelium of the gut is a layer of coarse wavy strands probably of collagen or of a closely allied material. This material extends into each fold of the typhlosole as a two-layered plate which is connected midventrally by a zig-zag ridge. The circular and longitudinal muscles lie outside the connective tissue layer. This tissue may maintain the lumen of the tract against variations in the coelomic pressure when the gut is empty.

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The circular muscles of the gut wall are not continuous with the corresponding bands within the typhlosole. The latter are arranged as sheets of muscles originating in the circular muscles of the septa, and lie external to the longitudinal muscles. The circular muscles of the gut wall (other than in the typhlosole) do not form a complete ring but cease dorsolaterally, at which level the longitudinal ones pass over them and continue into the typhlosole, where they come to occupy a position adjacent to the epithelium.

These longitudinal muscles are not of uniform thickness, being conspicuously thicker dorsolaterally, i.e. in the region bounding the epithelium adjacent to the typhlosole. Whether this thickening of the muscles is correlated with the forcing out of the secretion from the 'muroid' glands of the typhlosole is problematical (see *Figures 7.46–7.51*), but it has at least a superficial resemblance to the 'press' muscles involved in the formation of the peritrophic membrane in some insectan orders.

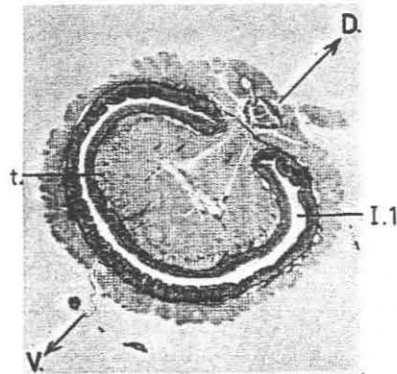


Figure 7.52. Transverse section through the second part of the intestine showing the smooth typhlosolar region. D, dorsal; V, ventral; t, smooth typhlosole; I.L., intestinal lumen

The ciliary mechanisms in the anterior part of the intestine appear to have no action in propelling the food along the tract as they would be incapable of generating the pressures required, even if the walls of the canal were in some way distended to allow them to beat freely. In the oesophagus of *Lumbricus* the ciliated part is short, and the ciliary activity here possibly serves to augment the muscular action of the anterior part of the oesophagus against the anti-peristaltic effects of the muscles of the glands and of the posterior part of the oesophagus. Even so, it seems reasonable to believe that the cilia evolved in relation to the backward passage of microcrystalline calcium carbonate from the oesophageal pouches and glands.

THE MECHANICS AND CONTROL OF GUT MOVEMENTS

The pressures developed by the muscles of the body wall are transmitted by way of the coelomic fluid to the gut wall, but since groups of segments along the length of the worm may be extended or in the process of becoming so, and others are contracted or contracting, a series of differing pressures occurs along the length of the body.

Now both the oesophagus and the intestine are tubular systems, with a light musculature in their walls, so that they can only be filled by some pumping mechanism capable of producing an even higher pressure than that of the coelomic fluid around them. Both the pharynx and the gizzard, in view of their heavy intrinsic musculature, would fulfil this function, being themselves largely resistant to changes in hydrostatic pressures.

Tentatively, it is suggested that the gizzard evolved as a secondary pumping mechanism in *Lumbricus* to force food along the intestine because of the loss of pressure in the oesophagus due to the interpolation of a ciliated portion in its middle third and to the presence of the crop. The triturating effects of the gizzard may have received undue emphasis in the past, for the materials within the gizzard do not appear to be physically different from those in the crop, and just as small stones and other debris occur in the gizzard so, too, are they present in the crop. The stimulus inducing contraction in both appears to be the presence of solid material within the lumen. A considerable pressure is

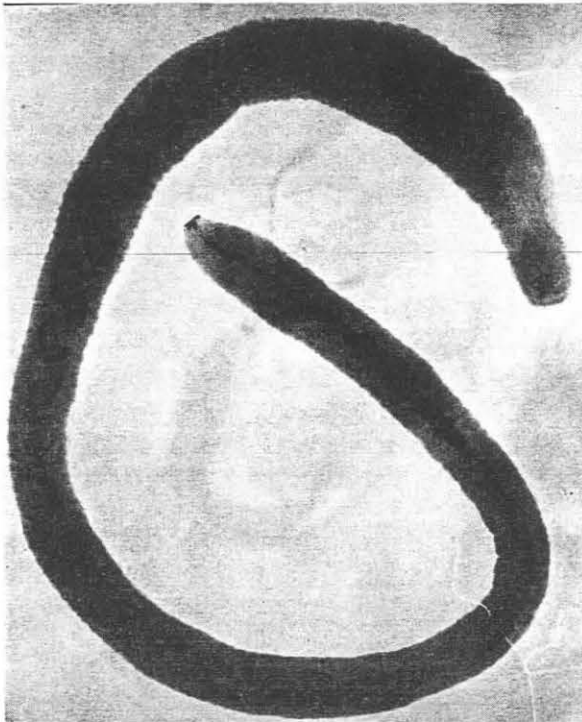


Figure 7.53. X-ray photograph of *L. terrestris* after a barium meal, as seen from the dorsal surface

generated during contraction of the gizzard and soil is moved down into the intestine at each contraction. Excised living portions of the crop-gizzard-intestine, ligatured at both ends, show that the eventual accumulation of soil in the intestine results in a great increase in pressure, which leads to a gradual thinning of the wall of the intestine, an increase in its translucency and,

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ultimately, its rupture during one of the contractions of the gizzard²⁷. Experiments with worms dissected under saline also show synchronous rhythmical dilatations and contractions along the short sacculated anterior section of the intestine.

On the balance of evidence it appears unlikely that the pharynx can exert the requisite force to push soil along the whole length of the gut, nor in view of other observations is the intrinsic musculature of the intestine likely to force soil effectively along its length.

Cine and X-ray photography of active worms shows that the intestine is thrown into broad lateral folds, each of which may extend over 3–5 segments (*Figure 7.53*). The folding is most enhanced when the longitudinal muscles of the body wall are contracted, as shown in *Figure 7.54a*. When the circular muscles of the body wall are beginning to contract the intestinal folds are stretched, whilst further straightening of the folds is evident when the circular muscles are approaching maximal contraction (*Figures 7.54e, 7.54f*). This

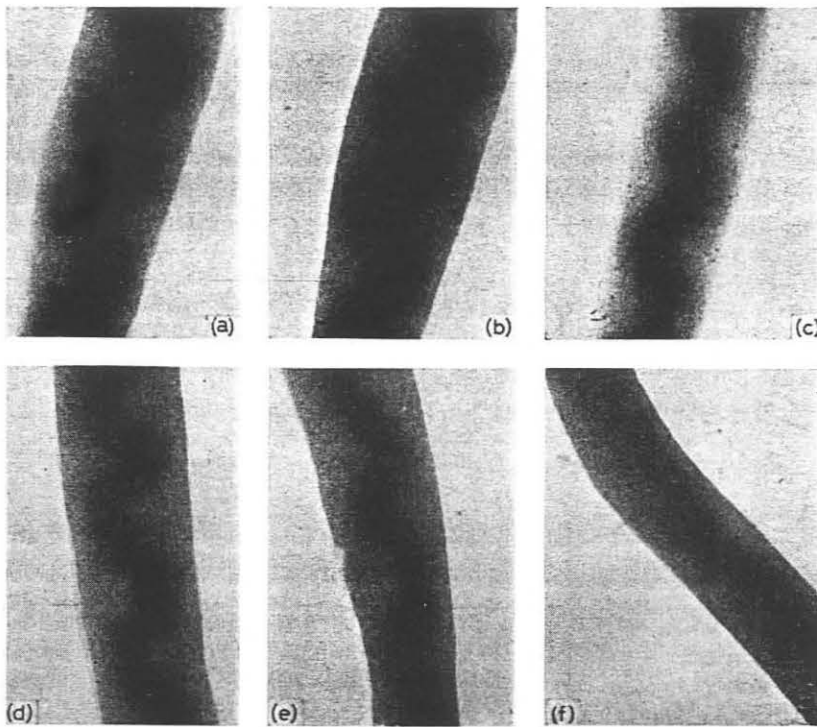


Figure 7.54. Changes in the pattern of part of the intestine of the worm during contraction and expansion of the body. a, longitudinal muscles of the body wall fully contracted; b–d, transitional stages of contraction of circular muscles of body wall; e, circular muscles approaching full contraction; f, circular muscles fully contracted

folding is a consequence, in part at least, of the need for local changes in the length of the segment or of a series of segments, while the canal remains freely extensible and the lumen is consistently maintained. Thus during contraction of the circular muscles of the body wall there will be at least a passive mechanical

straightening of the folds. From observations of cine film it is apparent that only on rare occasions is the unfolding of the gut sufficiently complete to eliminate all flexures and to produce a straight tube.

The successive waves of folding and unfolding of the intestine, and possibly of the oesophagus, are therefore associated with the constantly altering muscular configurations of the body wall, a feature schematically illustrated in *Figure 7.55*. Several simultaneous muscular waves pass along the body with consequent alternate lengthening and shortening of the segmental units. These appear to show some degree of localization of action by operating in groups. Thus at any one moment of time, for example, there may be two regions of the body (B1 and

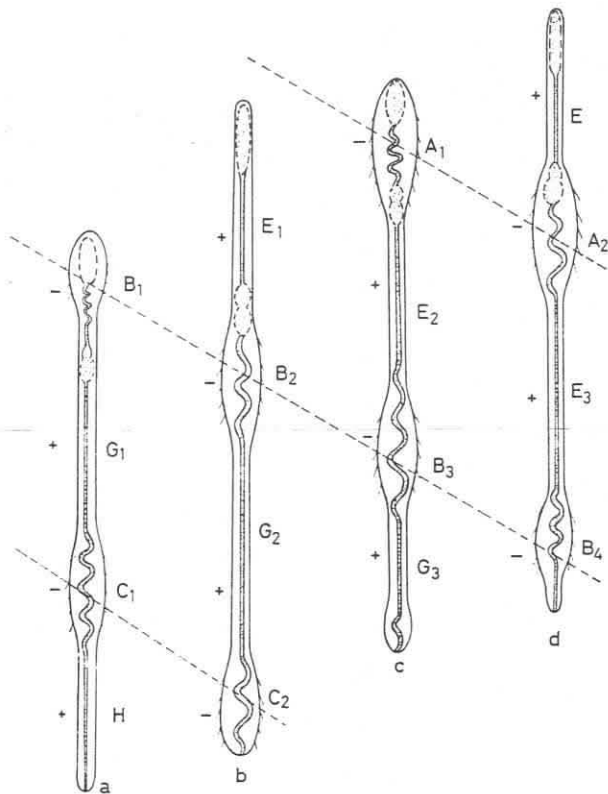


Figure 7.55. Patterns of muscular configuration of an earthworm, with concomitant pattern of the intestine and possibly of the oesophagus. The wavy line represents the gut in the folded condition; the straight line in a stretched condition; + represents regions of high pressure; - represents regions of low pressure

C1 in *Figure 7.55*) where the longitudinal body wall muscles are contracted, the chaetae protracted and the intestine maximally folded, whilst the intermediate (G1) and terminal portions (H) of the body have contracted circular body wall muscles, retracted chaetae and an unfolded intestine.

The highest pressures exerted on the coelomic fluid occur when the circular muscles of the body wall are contracted, i.e. when individual segments are

lengthened. Normally, in active worms the septa between the segments form bulkheads to the passage of fluid from one coelomic compartment to the next, and any tendency of the septa to bulge under pressure is controlled by their radial and circular muscles, possibly assisted by the oblique muscles. In this way transient local pressure differences are set up, which could not occur if the coelomic fluid was completely free to move up and down the body. From what has been stated in the foregoing paragraphs it may be deduced that on pure mechanical grounds regions of low coelomic pressures coincide with the folding of the intestine and *vice versa*.

At no time was occlusion of the *empty* gut evident on cine film when the circular muscles were contracting, i.e. when pressures would be highest. Accordingly, it would appear that there are counter-forces helping to resist these positive pressures, so as to maintain this lumen. Such forces may be developed by the radial muscles of the septa inserted into the peritoneum of the gut and being continuous with the circular muscles of the body wall. The thick 'collagenous'-type layer, lying internal to the circular gut muscles, may also contribute in this respect, as it is folded in unfed worms and passively extended in worms whose intestines are full of soil. On an *a priori* argument it might be supposed that the quantity of soil in the gut would influence the lengths of individual segments. For example, in a worm whose gut is well packed with soil the resistances offered to increased hydrostatic pressures would be greater and accordingly the segment would become longer (when the circular muscles of the body wall contracted) than if the same forces were applied to an empty gut. This does not seem to be borne out from observation, for the segments of fed and unfed worms lengthen to the same degree and this suggests that factors additional to soil are responsible. Further circumstantial evidence in support of the existence of counter-forces associated with the gut, which resist the positive pressures of the coelomic fluid, is afforded by the fact that there is no continuous defaecation of the soil through the anus when the worm is active. The existence of complete defaecations, in the form of casts, at one period during its diurnal activity suggests that there may be an alternative mechanism at play, for our unpublished experimental results show that the whole of the contents of the alimentary canal are voided once or twice in every twenty-four hours. By using ^{32}P as a marker in H_3PO_4 , mixed with soil, Parle²⁸ recorded that the time taken for full passage of 'soil and food' through the gut of *L. terrestris* was 11–12 hours, when burrows were being formed and the worms were not feeding. Experiments described later in this chapter (page 246) indicate that *L. terrestris* is primarily a surface feeder, but whether this time factor would apply to worms, whose primary source of nourishment is the organic matter in the soil, is questionable. The rate of passage of marked food through the gut of *L. terrestris* is about 20 hours²⁸, a view which is in agreement with the observations on *A. caliginosa*²⁹. Such continuously altering pressure systems as do exist in the worm are unlikely to be efficient in moving soil along the intestine, for if the localized pressures over a period of time are equated along the whole length of the worm, this will allow considerable reflux of the contents. Hence to assist in the propulsion of gut contents from mouth to anus there must be an overall pressure gradient anteroposteriorly. The existence of such a gradient has already been recognized³⁰, for in the anterior third of the body of an actively wriggling worm there is an average hydrostatic pressure of about 13.5 cm of water (range

2–29 cm of water) while the corresponding pressure in the tail end of the worm is 8.5 cm of water (range 4–19 cm of water). Additionally the gut shows peristalsis and appears to be under nervous and humoral control, although the rate and amplitude of these movements in Ringer vary greatly in different regions and in different individuals. Even so, there is reasonable unanimity that the pharynx, oesophagus, crop and gizzard are the most active parts. A number of authors have stated that the crop and gizzard contract rhythmically and that such movements are the results of propagated waves of contraction depending on local nervous reflexes. Stimulation of the anterior segmental nerves results in a distinct fall in tone of the gut muscles and this is produced by inhibitor fibres in the nerve. Conversely, stimulation of the anterior and posterior segmental nerves (the gizzard by posterior segmental nerves only) produces a rise in tone of the gut in the same segment, but in addition they also carry inhibitor tracts.

Less certain information is available concerning the movements of the intestine of the worm *in situ*, although when opened in saline this region invariably displays the most sluggish movements. Kymograph records of isolated intestine show a variation in rhythm depending on the species used. Thus in *L. terrestris* the contractions are comparatively brief, in *Allolobophora* slow tones appear and in *Dendrobaena* (= *Eisenia*) *venata* relatively sharp contractions are followed by slow relaxations.

The alimentary tract of *Lumbricus terrestris* is innervated by one set of nerves arising from the circum-oesophageal commissures, which form a plexus passing back between the epithelium and the muscle layers of the intestine. The second set of nerves pass up the septum to the gut and have their origin in the ventral nerve cord. The functioning of this double innervation system has been the subject of two interpretations. Wu³¹ believes that excitation of the nerves originating in the ventral nerve cord decreased the motility of the gut wall, whilst stimulation of the plexus derived from the oesophageal commissures increased this motility. The alternative interpretation put forward by Millott^{32,33} specifies that excitor and inhibitor fibres are both contained within the septal nerves, and the role of oesophageal nerves is not clear. From our observations, however, it would appear that both types of fibres also occur in the oesophageal nerve in as far as they innervate the buccal cavity. Stimulation of the ventral nerve cord, in addition to affecting the tone of the gut, also leads to increased secretion of protease enzyme to the gut lumen³⁴. The pathway involved in this response passes from the ventral nerve cord to the peritoneum, lining the inner surface of the body wall, thence through the ventral part of the septum to the plexus of the gut.

Functionally the system is undoubtedly a double one. Acetylcholine is synthesized by the gut nerves and under its influence the intestinal muscles of the earthworm contract, whilst a cholinesterase-specific enzyme has been demonstrated in the gut which is thought to be the enzyme responsible for the degradation of internally produced acetylcholine. Eserine increases the sensitivity of the gut but atropine exercises an inhibitory effect. Gut preparations kept in saline in the presence of eserine at 17–20°C release substances into the medium which are capable of causing contraction of other similar preparations.

Inhibition of the muscular movements of the intestine of *Lumbricus* is also an active process and the responses of the gut to the addition of adrenaline depend on (a) which part of the gut is subjected and (b) the concentration applied.

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The buccal cavity, pharynx and oesophagus are stimulated to contract by adrenaline in all concentrations. The posterior section of the crop, gizzard and intestine are either inhibited or stimulated by adrenaline according to the quantity added. Acetylcholine-induced contractions can be counteracted by large dosages of adrenaline.

Because adrenaline has no effect on the cooled gut²⁷ it has been considered that the action of adrenaline is to activate acetylcholine. By injecting adrenaline, acetylcholine, tyramine and ephedrine into the blood stream by way of the pseudohearts in *L. terrestris* it has been found possible to mimic the action of the nervous system, from which it is concluded that the nerves controlling the tone of the gut are cholinergic and adrenergic, and that the two systems are not potentiating but antagonistic. In Wu's³¹ view the nerves in the septa are of the adrenergic variety, since their action is abolished by ergotoxin.

Any system of the type which operates under a force pump principle must be supplied with regulating and sealing devices to prevent too rapid passage of food through the system. Such sealing devices occur in the pharynx and the gizzard, as we have already seen, whilst the crop with its complex of muscled folds and channels probably assist materially in regulating the speed at which the soil passes into the gizzard. Moreover, the alternate stretching and folding of the gut would doubtless function in the same way. Terminally the body of *Lumbricus terrestris* is flattened dorsoventrally and the anal aperture is surrounded by a sphincter valve.

In aquatic annelids the muscles outside the blood sinus contract antiperistaltically and tend to hinder the transport of gut contents towards the anus, and the contents of the alimentary canal are transported by its cilia which beat towards the anus³⁵. Whilst being prepared to accept the validity of this assumption, work on feeding and digestion in Terebellids shows that the importance of body wall movements should not be underestimated. Strong constricting and segmenting movements in the fore and hind stomachs of terebellids have been reported³⁶ but no comparable movements were observed in the intestine of the earthworm when opened up in Ringer, or on cinefilm of active worms³⁷.

It is commonly stated that in coelomate animals the movements of the gut walls are independent of those of the body wall, owing to the intervention of a fluid-filled space. In the light of the observations outlined here of the gut *in vivo*, together with evidence from work on Terebellids, it would appear that the lengthening and shortening of the body wall during locomotion does influence the unfolding and folding of the gut. Independent movements of the gut in coelomates, with its dependence on intrinsic musculature alone, occur when the body wall ceases to be directly involved in locomotory activity, e.g. in animals with rigid exo-skeletons (as in the arthropods) or when the body is supported by an endo-skeleton whose component parts are not deformed by external pressure changes (as in echinoderms), and whose outer body wall is consequently only minimally affected during progression.

GUT ENZYMES

Much of this section is taken from Laverack²⁵ and is included for completeness.

The wide range of food ingested by the worm requires a number of enzymes to

cope with its diet. Reference has already been made to the secretion of protease from the pharynx in *Lumbricus* and *Allolobophora* and of amylase in *Eisenia* but most of the enzymes are restricted to the intestine. The secretory cells have a brush border, and by incubating watery extracts of the intestine with starch, methyl butyrate and with gelatin or casein respectively an amylase (at optimum pH of 6.8–7.0), a lipase (at pH 6.4–6.6) and a weak protease (pH 8.0) have been shown to be present. It is alleged that protein is digested in the crop of *Pheretima* but there is little evidence of enzymatic activity in either the crop or the gizzard of other species. Further work³⁴ shows the production of a protease in the anterior region of the intestine, which has a rennin-like action, clotting milk containing calcium as a co-factor. Electrical stimulation of the segmental nerves results in considerable increase in the quantity of the secretion. Incubation of powdered cellulose in the gut extracts results in the production of soluble reducing sugars and in fact the presence of cellulase has been confirmed in the anterior intestine³⁸. This means that the cellulose of plant walls can be utilized. Acetyl glucosamine is found as an end-product of digestion when intestinal extracts are mixed with chitosan hydrochloride at pH 5, suggestive of the presence of a chitinase. The occurrence of both enzymes has been demonstrated in a number of worm species, but in others only cellulase has been found³⁸. Recent experimental evidence²⁸ supports the view that cellulose is hydrolysed by enzymes of the gut, for the length of time that the food remains in the gut is inadequate for much microbial action to occur unless there are many cellulolytic organisms, which does not appear to be the case. Chitin digestion is more problematical, for although the worm produces chitinase, there are many organisms in the gut which could attack chitin in the numbers present. Even so the quantities of these two substances broken down in the gut requires further investigation for much occurs as residues in casts. Further work indicated that lichenin, obtained from lichens, is hydrolysed by gut extracts, presumably by enzyme action. The upper and lower pH limits in the intestine of *Lumbricus terrestris* are 6.3 and 6.6 respectively, in *Allolobophora savignyi* the range is from 6.49 to 7.32 when the anterior part of the intestine is most acid.

Mobilization of digested products. The products of digestion occur in the urine, blood and coelomic fluids, but in general the higher molecular weight organic compounds such as glucose, proteins and amino acids in the coelomic fluids are at a very low concentration compared with the blood values for the same materials. Such results may be interpreted as being due to the rapid removal of nutrient materials from the coelomic fluid by the tissues which are bathed by this fluid and the concentrations of these substances always tend to be low. Alternatively the chemicals may be reabsorbed into the blood system which then transports the necessary raw materials to the tissues. This is unproven, but since the intestinal wall is well supplied with blood vessels it might well be a possibility.

The intimate association of the chloragogenous tissue with the intestinal wall has suggested the chloragocytes as the intermediary site of metabolism. These cells contain many obvious granules consisting of peripheral concentrations of phospholipids and ethylene groups. The pigmentation of the chloragogenous tissue is due to a chromolipid which consists of a phospholipid combined with a yellow-brown material which spectrophotometric analysis

suggests may be a complex mixture of substances in equilibrium³⁹. An alternative explanation for this pigmented material is that it consists of an oxidized phospholipid which polymerizes with purines within the cell⁴⁰. The possibility that the products within the cell are of alimentary origin is suggested by the distribution of alkaline phosphatase at the periphery of the cell adjacent to the chloragocytes and indicative of active transport of absorbed substances across the cell boundaries. Once having been absorbed the next problem of transportation of this material to tissues requiring it has to be solved. It has been suggested that the chloragogen cells are able to leave the site of origin on the intestinal wall and to wander freely in the coelomic cavity. Whilst it has been stated that the cells are 'able to pass freely' in the coelomic cavity no information is forthcoming as to how this is effected bearing in mind that the septal walls form bulkheads and do not allow the passage of even coelomic fluid from one segment to the next. The concentration of chloragogenous tissues around a wound within a few hours of wounding does suggest the possibility of a migration, but might it not be produced by rapid proliferation of tissue? Presumably such cells are responsible for the scar tissue and for regenerating new tissue utilizing the stored products of the chloragogen cells. At the site of the wound the cells disintegrate and discharge lipid substances into the region. This activity becomes maximal after a few hours and returns to normal in a period of two or three days. The polysaccharide glycogen occurs in large quantities in the chloragocytes and may act as an energy supply for the regenerating region. At the distributional level it seems unlikely that all chloragogenous tissue acts as a liver, for its cells also occur in abundance along the oesophagus and there is no evidence whatsoever that absorption of food materials takes place in this region of the tract.

In unwounded animals it has been suggested that when the chloragogen cells contain food materials they wander through the coelom and as they do so they autolyse and the inclusions, glycogen, fats, etc., disappear into solution in the fluid. Whilst the body fragments are ingested by amoebocytes the fate of the chemical substances released remains untraced. Supporters of these views thus consider that the chloragogen is liver-like in its action, whereby it functions as a homeostatic device to maintain a constant level of circulating substances^{39,40}.

WORM CAST PRODUCTION AND FEEDING IN RELATION TO HABITAT

One of the significant features associated with earthworms is their production of worm casts. Nearly two hundred years ago earthworms were described as the 'great promoter of vegetation' by Gilbert White of Selbourne, and almost one hundred years ago Darwin⁴¹ estimated that the annual worm cast production on two grassland sites was 7.5 and 16.1 tons per acre, so that the role of the earthworms as a natural biological mechanism for the turnover of soil in the form of worm casts has been historically recognized for a considerable time. This cast production is one of the most important effects of earthworms on soil, for from evidence of wet sieving techniques used to evaluate the structure and strength of crumbs it has been found that worm-worked soil contains more crumbs of soils which do not break down when wetted than do soils unworked by worms. The stability of casts from land under grass, according to some investigators, is much greater than those from land under straw crops, but

whether this is valid is questionable for this is equally true for uncast soil and may be independent of earthworms¹⁵.

Various interpretations have been put forward to account for this property of stability^{15,16}. Plant residues passed through the tract along with the soil have been implicated as reinforcing mechanisms, and the claim has been made that the stable qualities vary in relation to the feeding behaviour of different earthworm species. Experimental attempts to produce aggregates from soil and broken down roots have not been successful.

An alternative view put forward suggests that intestinal secretions of the worm, or of bacteria or of microflora within the gut are responsible for the adhesive properties of the soil particles which give stability to the casts. This view of the function of the intestinal secretions does not gain much support from the differences in the stability of casts from grassland and arable land. Many bacteria produce levans and dextrans, and these polysaccharide molecules are known to bind quartz particles and clay particles. The bacterial population in the earthworm gut is some 1,000 times greater than that of the surrounding soil, so that these gums may be responsible for binding the gut contents as casts, although other workers have rejected this idea as they could find no direct relationship between the proportions of water soluble aggregates in casts and soil and the numbers of bacteria present. Moreover, the amount of polysaccharide gums necessary to produce good aggregation is probably considerably higher than occurs in the field. An alternative cementing action has been attributed to calcium humate which is synthesized in the worm's gut from ingested organic matter and the calcite secreted by the calciferous glands, or other calcium source derived from the food. Even so, casts retained their high stable qualities even after treatment in acidified H_2O_2 , which would be expected to oxidize both calcium humate and the polysaccharide gums.

Emerson⁴² has indicated that stabilization of soil crumbs is to be attributed to a long chain polymer, which links the external surfaces of orientated groups of clay crystals to each other and to food grains. Parle⁴³ found that the number of fungi in fresh casts was not different from that in soil although their germinating spores were common in the former and rare in the latter. This indicates an inhibitory factor to germination in soil, which is absent from worm cast soil. The length of the fungal hyphae increased greatly with age up to fifteen days, after which they declined. Correspondingly, the stability of the casts increases with the length of the fungal hyphae up to fifteen days, and this may be attributed to hyphal mechanical strengthening. After about fifteen days the stability of the casts decrease, as determined by the ratio of permeability before and after sodium saturation.

Of the British lumbricid worms only a small minority produce surface casts of any significance. It is then pertinent to ask what are the necessary prerequisites for their egestion. As we have seen, soil is the principal component of the excreta, hence it must be taken into the gut either passively during burrowing or be actively acquired during feeding, and for either course to be followed the casting lumbricid has to obtain access to it.

The ability to penetrate into such a medium as soil requires adaptive mechanisms to achieve this purpose, and an analysis of lumbricid dimensions may not be out of place in this connection. The range in length and diameter, together with the calculated means of British lumbricids, with the exception of

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Allolobophora rosea f. *macedonia*, are diagrammatically represented in Figure 7.57, where they are arranged, from left to right, in increasing magnitude of calculated mean lengths. In passing from left to right it is seen that the first part of the curve is relatively flat, i.e. from *D. octaedra* to *D. rubida* f. *subrubicunda* and in general their calculated mean diameters are at or below 4 mm, with the exceptions of *E. tetraedra* f. *macrura* and *E. foetida* which were measured across their clitella and accordingly represent a false value of the diameter of their bodies as a whole.

The succeeding part of the curve rises more sharply and includes *A. caliginosa* to *D. veneta* f. *typica*. The increased values of the mean lengths of this group of worms are in substantial agreement with the increased means of their diameters (with the exception of *A. caliginosa* as measured across the clitellum) and now range from 4–6 mm. Finally the curve for mean lengths rises more steeply and includes *A. nocturna* and *L. terrestris* with *A. longa* and *O. cyaneum* being transitional species, but all are characterized by having mean diameters which exceed 7 mm. On this basis it is convenient to refer to them as 'small, or thin, worms', 'medium-sized worms' and 'large, or fat, worms' respectively.

The question of dimensional relationships with respect to changes between length and circumference using as a model a cylinder of variable dimensions and fixed volume has been considered by Chapman⁴⁴ and in his example he refers to a cylinder of 'volume of 15,700 cubic units, a radius of 5 units and a length of 200 units' being proportions not unlike those of a 'worm'. The results of varying the dimensions of such cylinders are tabulated below:

Radius	Circumference	Length	Volume (= a constant)
2	12.5	1,260.0	15,700
3	18.9	555.6	15,700
4	25.1	312.4	15,700
5	31.4	200.0	15,700
6	37.7	138.9	15,700
7	43.9	102.1	15,700
8	50.3	78.0	15,700

According to Chapman⁴⁴ the percentage change in length of a cylinder of variable dimensions is accompanied by half that percentage change in circumference. The basis for this being that if a small change of $+\delta l$ occurs in l the percentage change is then $+\frac{100\delta l}{l}$ and the corresponding change in c is $\frac{100\delta c}{c}$ where

$$\frac{c+\delta c}{c} = \frac{\sqrt{l}}{\sqrt{l+\delta l}} = \left(\frac{1+\delta l}{l}\right)^{-\frac{1}{2}}$$

For relatively small values of δl this gives

$$1 - \frac{\delta l}{2l} \text{ leading to } \frac{\delta c}{c} = -\frac{\delta l}{2l}$$

Hence the percentage increase of δl in l is accompanied by a percentage decrease δc in c given by

$$\frac{100 \delta c}{c} = \left(\frac{100 \delta l}{l} \right)^{-1}$$

This is operative only when δl (and, therefore, δc) is small, or in biological parlance, is referable to small changes occurring in an individual.

In cylinders of constant volume, where circumference changes are of greater magnitude, $\propto 1/\sqrt{l}$, and the effects of such changes on the lengths may be seen by comparing cylinders having mean radii of 3, 5 and 7 units and whose circumferences are 18.9, 31.4 and 43.9 units respectively (*Figure 7.56*). If, for example, the circumferences of these three cylinders vary by ten units, about their respective means, it is evident that increases in length within this range become progressively less from cylinders of small circumference to those of larger circumferences. Or, in relation to worms for a given absolute change in length of the circular muscles the change in length of the longitudinals produced by it may be great or small according to whether l/r is at its greatest or smallest⁴⁴.

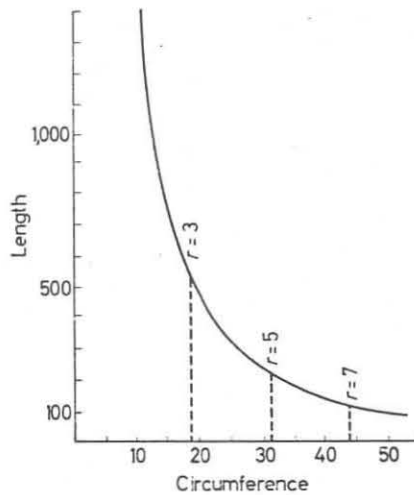


Figure 7.56. Graph showing the relationship between the length and circumference of a cylinder of fixed volume

Since the smallest change in length of the worm for a fixed change in length of the circular muscles occurs when the animal is at its thickest it would be expected that burrowing worms would carry out their burrowing when thick and not when thin. In other words, it is mechanically sound for burrowing animals of cylindrical form to be 'fat', as in our large size group. By this means they would be able to force soil particles aside more efficiently. Fuller discussion on these matters is given elsewhere^{30,44}.

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Conversely, if a lumbricid has a small circumference, i.e. is thin as in our small size group and possibly in the medium size group, then during crawling it will for each fixed contraction of the circular muscles progress farther, size for size, than if the body is thick. By the same token, and because it is unable to increase its circumference to anything of the same degree as a 'thick' or 'fat' worm, it will be less efficient at burrowing.

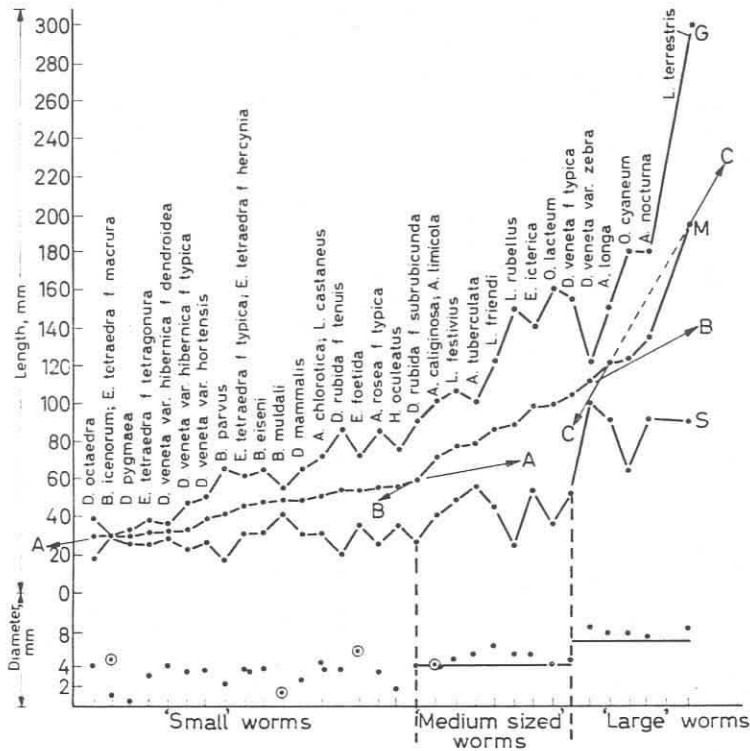


Figure 7.57. The dimensions of British lumbricids, shown in increasing calculated mean lengths from left to right. The mean lengths (*M*) are shown together with the maximum lengths (*G*) and the minimum lengths (*S*). The lines AA refer to the worms which conveniently fall into the 'small size group', BB to worms of the 'medium size group', and CC to those of the 'large size group'. The mean diameters of the worms are given below their lengths, and a dot within a circle indicates measurement across the clitellum.

Realizing that thin worms do, however, occur in soils, it is necessary to distinguish between those species which 'actively' construct burrows or shafts in the soil, whether these be temporary or permanent, and those recognized as surface forms. The latter would appear to utilize *existing* spaces between soil particles, or clumps thereof, and hence their movements are much more random and superficial than are those of burrowers. To all intents and purposes,

these surface forms fall into the category of 'crevice faunas' and are able to exploit such habitats by virtue of their thinness. Equally, they are able to insinuate themselves beneath stones, in dung pats or leaf litter, compost, etc. With increase in size, as in our medium sized groups, they become more efficient at utilizing soil crevices, even enlarging them, and in this respect may be considered as transitional forms between those which are 'crevice dwellers' *in sensu stricto* and the burrowing types.

In principle, if the size of the worm is a reflection of its ability to penetrate and move through soil it seems feasible for the immature stages of the 'medium' and 'large' size group, in particular, to exhibit a different vertical distribution in the soil when compared with their corresponding adults. Equally, if the issuing immatures of one species are larger than those of another, even though this size difference is not maintained to the adult stage, then the larger immature stages may occur at greater depths than the smaller ones. Confirmatory evidence of this maxim is afforded from the work of Satchell⁴⁵, who reported that both mature and immature stages of the species (viz, *A. caliginosa*, *A. chlorotica*, *A. rosea*, *O. cyaneum*, *A. nocturna* and *L. terrestris*) in a Rothamsted pasture were collected in the top soil; below about ten inches depth only large mature worms were found. Satchell (*in litt.*) also wrote that newly hatched *L. terrestris* only occur in the top few inches of soil in the locality of Grange-over-Sands. It might be suggested at this point, however, that such young worms occupy the superficial layers of the soil and are absent from the deeper subsoil because they derive their nutriment from soil organic matter. On the basis of the present argument it seems more likely that small worms are structurally ill adapted for burrow formation, but before being categorical on this point investigations on differential growth changes in different species in relation to depth of penetration in the soil are necessary. Nevertheless, the size and distribution of cocoons is of some interest in this respect. *L. terrestris* and *O. cyaneum*, for example, produce smaller cocoons relative to the size of the adult than does *A. longa*. Under experimental conditions it has been established that in general only one worm emerges from the cocoons of these species, and this is also so for other species of *Lumbricus*, *Allolobophora caliginosa*, *A. chlorotica*, *A. rosea* and it is possible that the emerging individuals will reflect the size of the cocoons. The cocoons of *A. chlorotica* are found in the top two inches of the soil, those of *A. caliginosa* at about one and a half inches, and those of *A. rosea* between two and three inches⁶. The adults of these species live from 4–9 inches below the surface. Cocoons of *L. terrestris*, *O. cyaneum* and *A. longa*—all the products of shaft producing adults extending down from thirteen inches to four feet or more—also occur in shallow soil ranging from three to six inches below the surface⁶. Obviously then the adults of these species migrate into the shallower regions to deposit their cocoons, so that the emerging immatures are best situated to move through the soil to obtain the required nutriment.

If, on the other hand, more than two worms are produced within each cocoon, as appears to be so for *E. foetida* (1–8 produced) and *D. rubida* f. *subrubicunda* (1–4 produced)⁶ our initial premise is no longer true and it could be reasonably expected that such cocoons would be more superficially distributed under natural conditions, than are those of the species referred to in the preceding paragraph. There is an obvious need for an extension of this sort of

work together with additional data on the feeding habits of immatures under field conditions.

A correlated feature associated with differential sizes of lumbricids and their ability to colonize various habitats is that the smaller the lumbricid the greater the surface area/volume ratio when compared with larger lumbricids. And in the absence of localized and specialized structures gaseous exchange takes place through a thin film of moisture maintained at the interface between the air and the skin, and water is also lost through the skin surface so that the greater the surface area to volume the more rapid would be these losses. The mechanical inability of 'thin' worms to burrow deeply would therefore restrict them either to the aquatic medium or else to areas of very high humidity to prevent desiccation.

Helodrilus oculatus of the 'small' forms is recorded from black mud in the River Thames and the bottom of Lough Mask, and it is tentatively suggested that movement through such water-saturated, finely particulate material presents rather a different mechanical problem from burrowing into soil. The occurrence of this species at depths of 8–15 feet in the Roman remains at Verulamium is more enigmatical, and Dobson and Satchell⁴⁶ consider the possibility of the worms entering the ditch in Roman times before it was filled in and having 'continued to breed there ever since'. Support for this is given by the presence in their vicinity of seeds of *Carex* sp., typically plants of marshy situations, and highly indicative of it being a suitable habitat in Roman times. Satchell (*in litt.*) informs me that this species was burrowing in 'compact, tenacious clay showing no trace of crevices or crumb structure'. Under these circumstances, its method of burrowing is a puzzling feature and we may have here a case of a worm literally 'eating its way through the soil'.

According to these authors the similarly proportioned *Bimastos icenorum* and *Bimastos muldali* (= *Allolobophora minima*) appear to have been found in the same type of habitat as *H. oculatus*. *B. icenorum* and *H. oculatus* were collected from 'clayey soil under rotting sedge' at Wicken⁴⁷ and a specimen of *B. muldali* from among preserved *H. oculatus* from the Thames and Nottinghamshire. Some of the sites occupied by these three species are suggestive of conditions of poor aeration and their exploitation of such anaerobic habitats implies a facultative ability to absorb oxygen at very low tensions and that these small species may occupy habitats which may be closed to other lumbricids.

Of the remaining species in this group some are associated with aquatic habitats, e.g. *Eiseniella tetraedra* f. *macrura*, or are amphibious as are *Eiseniella tetraedra* f. *typica* and *E. t. f. hercynia*, although the *typica* form has been reported in some numbers from 'moist, but not wet, soil in a permanent pasture in Perthshire'¹⁰. Most records of these two forms are from wet soil (depth not specified) under stones and moss on river and stream banks, mostly covered with water or purely aquatic habitats. Species like *D. pygmaea*, *D. rubida* f. *tenuis*, *D. venata* var. *hibernica* f. *typica*, *D. rubida* f. *typica*, *D. mammalis*, *B. eiseni* and *B. parvus*, have strong associations with damp to very wet habitats, which may be supplied by coverings of moss, leaf litter, by living in caves (e.g. *D. rubida* f. *typica*) or under stones, in the surface layers of moorland and bog soils (e.g. *B. eiseni*), or in such specialized habitats as decaying logs or stumps (e.g. *B. parvus*). Of the larger species of this 'small' size group, *E. foetida* occurs in manure, compost heaps, under dead leaves and lives in well creviced soil rich in

organic matter. At night time it crawls over the surface where compost has recently been spread and it appears that organic matter constitutes the main food source. *Lumbricus castaneus* is also a surface form and, like *A. chlorotica* and *A. rosea* is capable of pushing itself between soil particles to a depth of usually not more than four inches, and is also found under dung pats and among grass roots. That they do not form well defined burrows is also indicative of their surface feeding habits, and it is unlikely that these, like the other components of this 'small sized' group, will contribute to surface casts as they do not appear to ingest large quantities of soil. *A. chlorotica* is a species of considerable interest in that it represents a transitional form from land to water. It is often numerically abundant in pasture and arable land as well as in gardens, it can be found in wet soils adjacent to lakes, ponds and rivers, and is reported from Lake Windermere living under six feet of water. It is also recorded from semi-fixed dunes in Anglesey, which are xeric in the summer. *A. rosea* and *L. castaneus* are also frequent on banks of rivers, and lakes in limnic localities as well as on marsh banks.

Of the species, varieties and forms in the 'medium size' group, information on the ecology of *E. ictérica* and *A. tuberculata* is negligible, but the remaining forms appear to conform to a similar ecological pattern as the previous group, i.e. mainly surface dwellers with a frequent association with superficial material, e.g. litter, dung or stones. *A. caliginosa* and, probably, *A. limnicola* make multidirectional, ramifying burrows at about 4–9 inches below the surface in much the same way as do *A. chlorotica* and *A. rosea*. They occur in most habitats and are particularly frequent in cultivated soils and light loams, and the ramifying nature of the burrows may possibly be due to their following 'lines of least resistance' in the soil. *A. limnicola* is probably not so clearly divorced from the aquatic habit for it does occur on marshy and wet soils. Leaf litter does not appear to be a favoured dietary requirement of *A. caliginosa* and under field conditions preference is shown for root residues rather than for dung or dead herbage. Like most lumbricids, however, it can be fed successfully on dung in the laboratory and a mature worm can consume 20–24 grams in a year. *Lumbricus rubellus* lives either in leaf litter or moves into the surface layers of the soil and is the species most frequently found aggregating beneath dung in the upper moorland type of habitat. Similar habitats are occupied by *L. friendi* and *D. veneta f. typica* although the latter appears to be more specialized as it congregates under decaying leaves around rhubarb crowns.

In general, on the information available, most members of this group are capable of entering the soil, mainly by insinuating themselves into existing spaces and not by active burrowing. It is probable that they feed on decaying organic matter from superficial deposits and casting is then likely to be unimportant.

The 'large size' group of lumbricids includes five species as judged on a consideration of their lengths and diameters and on their behaviour in soil. One of these, *D. veneta* var. *zebra* is rare in Britain, and beyond stating that it is terrestrial our knowledge is meagre. The remaining members of the group are separable from those in the preceding two groups in that they form well defined shaft-like burrows. Those of *O. cyaneum* are temporary and reach from about six to twenty-two inches below the surface, whilst those of *A. longa*, *A. nocturna* and *L. terrestris* are fairly permanent. The burrows of the two *Allolobophora*

species range from about twelve to eighteen inches below the surface and those of *A. nocturna* are complex with numerous openings connected by branches which run horizontally. Those of *L. terrestris* form vertical, unbranched channels and may extend downwards to four or six feet, and sometimes even deeper, and doubtless this ability to penetrate deeply is associated with their body form. Prior to publication this paper was sent to Dr. J. E. Satchell for his comments. He drew my attention to his Ph.D. thesis (1953) in which he refers to depth distribution of earthworms in a Rothamsted pasture. He states that '*A. caliginosa*, *A. chlorotica* and *E. rosea* (= *A. rosea*) were found in the soil proper while the three other species (i.e. *A. nocturna*, *O. cyaneum* and *L. terrestris*) present penetrated into the underlying clay'⁴⁵.

The feeding habits and diet of *O. cyaneum* are not known with certainty and the habit of crawling over the surface of grassland during daylight after heavy rain may be misconstrued as a 'feeding mission'. It is more likely to be a reaction to the flooding of its burrow, the effects of which we have referred to earlier. This species is widespread in the British Isles but is never abundant, and as such can have little effect on surface cast production. The most detailed information on feeding in this group of lumbricids is available for *L. terrestris*, and Darwin's observations, subsequently substantiated by other workers, show that it draws leaves and other materials, including stones, into its burrow. At the entrance to its burrow leaves and blades of grass are found projecting vertically, in addition to cast soil. A series of interesting experiments carried out in apple orchards at Wisbech by Raw⁴⁸ are worthy of comment in as far as they shed light on the feeding behaviour of earthworms of the 'medium' and 'large' size groups. Common species which occur in such situations are *L. terrestris*, *L. castaneus*, *A. longa*, *A. caliginosa*, *A. chlorotica*, *A. rosea* and *O. cyaneum*, and in laboratory experiments it has been observed that *L. terrestris* was the only species regularly to bury apple leaves in the soil, when they were placed on its surface. This agrees with the known habits of the species, though occasional specimens of *A. longa* also behaved in like manner. In field experiments a population of *L. terrestris* of 2,000 lb. per acre buries over 90 per cent of the leaf litter that falls in orchards. Their activity could account for the observed amounts of leaf litter removed during the winter, and differences in the amounts removed in different orchards were in proportion to the populations of *L. terrestris*. Raw also demonstrated that more leaves were buried in arable orchards than in grass orchards, and this may be due to the availability of grass as an alternative source of food or to increased difficulty in finding apple leaves when grass is present, or to the difficulties in burying leaves under grassland conditions. Evidence was forthcoming from grass orchards that the amount of surface vegetation affects the number of leaves buried.

Other workers have demonstrated that in fresh litter leaves of beech, ash or dog's mercury are the most favoured by *L. terrestris*, followed in turn by those of maple, oak, horse chestnut, lime, willow and false acacia. Conifer 'needles' are the least acceptable. When the leaves undergo decomposition the feeding preferences of the worms alter to willow, false acacia, oak, lime, beech, maple and horse chestnut. Various reasons for this selection, such as the shape and texture of the leaves, their protein content and flavour, have been postulated. There appears to be little direct evidence for any of these claims, but it is suggested that the choice of grazing preferences at different times of the year

may be indicative of changes in the chemical constitution of the leaves and the accumulation of various metabolic products in them. As decomposition of different leaf types proceeds and undesirable by-products are leached out, the grazing preferences of the worm change. Alkaloid substances or noxious aromatics are not readily ingested, 50 per cent acceptance being noted at a concentration of 0.01g/20g gelatine, but above this level there was complete rejection. Such acids as phosphoric, tartaric, citric, oxalic and malic acids which occur in plants are acceptable in low concentrations but not at high concentrations. Both green and dead leaf fragments have been collected from the gut of *L. terrestris*, although the epigeal parts are eaten only, according to one authority⁴⁹, when the worms lack vitamin A, which is thought to be necessary for the secretion of their saliva.

L. terrestris is a surface feeder and the physical conditions under which they feed requires more thorough investigation. The critical temperature under which they come to the surface in early autumn is about 5°C, but in late winter this figure may drop to 0.4°C. In orchards, according to Raw, leaf burial depends on soil temperature and this process ceases at 2°C, which is about 1.6°C lower than the minimum weekly temperature of Wisbech soils in winter. No quantitative data on humidity conditions appears to be available and most authors suggest that the soil or vegetation cover should be 'wet'. Light intensity has been more critically analysed and optimum conditions for feeding appears to be 0.02 foot candles or less. However, after long spells of unfavourable conditions worms have been seen to feed on the surface nearly twenty minutes before dusk in light of 0.13 foot candles, which is suggestive of a response to a hunger stimulus and adds further support to the view that *L. terrestris* is almost entirely a surface feeder. The acquisition of soil by this species may well be a passive process associated with burrowing, and the ingestion of soil micro-organisms and decaying remains of animals may be incidental contributions to the dietary requirements.

The two remaining species in this 'large size' group of lumbricids are *A. longa* and *A. nocturna*, both of which have been observed to feed on the surface, albeit occasionally when compared with *L. terrestris*. *A. longa* under laboratory conditions has been observed to eat leaves, but a study of the gut of naturally occurring field populations indicates a preference for root residues, fungus mycelia and compost.

Of the common field species in Britain only three, viz. *L. terrestris*, *A. longa* and *A. nocturna*, produce casts on the surface, and of these only the two *Allolobophora* species contribute materially to the weight of surface casts produced. Some idea of the quantity of soil removed in this way may be gathered from the statements that 'one hundred to three hundred tunnels per square metre have been counted in European pastureland, and the tunnel volume under grass has been claimed to be as high as 0.05 cc per cubic centimetre of soil occupying as much as 67 per cent of the soil air space. The average total soil consumption by earthworms in pastureland in western Europe is probably about 6 kg/sq. m per year, of which about two-thirds is transported to the soil surface as worm casts, the remainder being voided in soil crevices'¹⁶. What is also surprising is that, on size considerations and the depth of penetration in soil, our largest and most deeply burrowing species, *L. terrestris*, should occupy a subordinate position to the smaller *Allolobophora* species in cast production, bearing in mind that the

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latter cast between September–December and March–May, while *L. terrestris* produces casts throughout the year.

On purely theoretical grounds and on the assumption that their behaviour patterns in the soil are similar, approximate calculations of the volume of the gut of the largest, average and smallest of these three lumbricid species, on the basis that the diameter of the gut in each is half that of the body, yield the following data:

Largest worms	Gut volume (mm ³)
<i>L. terrestris</i>	3,329.4
<i>A. longa</i>	1,664.7
<i>A. nocturna</i>	883.1
Average sized worms	
<i>L. terrestris</i>	2,164.1
<i>A. longa</i>	1,331.8
<i>A. nocturna</i>	662.3
Smallest worms	
<i>L. terrestris</i>	998.8
<i>A. longa</i>	998.8
<i>A. nocturna</i>	441.6

In the smallest worms the intake of soil should be the same for *L. terrestris* and *A. longa*, and this is more than twice the quantity taken in by *A. nocturna*. In average sized worms *L. terrestris* has a gut capacity of about 1.6 times that of *A. longa* and more than three times that of *A. nocturna*, whilst the corresponding ratios for large worms are 2:1 and 4:1 respectively.

These theoretical implications are not, however, in accord with observations in the field or laboratory, so that cast production would appear to be related to the behavioural patterns of these oligochaetes. On this score the following interpretations are possible. All three species ingest soil to the full capacity of their gut, and whereas *Allolobophora* species live sufficiently near to the surface to undergo frequent migrations to defaecate, *L. terrestris* being buried deeper in the soil will deposit in, or en route to the surface, with a final elimination of the remains at the burrow opening. But this would only account for the fact that the casts of *L. terrestris* are smaller than are those of *A. longa* and *A. nocturna*, and would bear no relation to their feeding habits. From the evidence it appears that *L. terrestris* is a surface feeder on leaves and that the quantity of soil ingested either passively or actively during burrowing will be small relative to the total capacity of the gut. In contrast to this the available information on these two *Allolobophora* species indicates that they feed on material within the soil and that surface feeding on leaves is incidental. The dietary requirements within soil are obviously diffuse and, in order to obtain the necessary quantities, animals dependent on it will require to range widely and to take in considerable volumes of soil at relatively frequent intervals. This would imply more frequent defaecations and, when compared with *L. terrestris* which obtains its food in bulk and in concentrated form, i.e. as leaves, a more rapid turnover of soil through the gut and a greater production of surface casts.

Again we have no direct evidence that this is the pattern in *A. longa* and *A. nocturna*, but feeding preferences in relation to habitat selection of all the lumbricids might prove an interesting field for research, and much requires to

be done on the physiology of digestion, which is undoubtedly a correlated feature.

I am much indebted to Dr. J. E. Satchell, Mrs. A. M. Hughes, Mr. T. E. Hughes, Dr. K. Eltringham and the Editor, Dr. John Carthy, for reading the manuscript of this paper and for their helpful suggestions and comments. Mr. R. Reed was responsible for the photographic work in this paper and I am grateful to him for his co-operation.

NOMENCLATURE OF BRITISH LUMBRICIDAE

To prevent confusion the names of the lumbricids used in this account follow those given by Gerard, B. M. (1964) in *Lumbricidae (Annelida) No. 6 Synopsis of the British Fauna*. The Linnean Society of London.

- Eisenia foetida* (Savigny, 1826)
Allolobophora caliginosa (Savigny, 1826)
Allolobophora longa Ude, 1855 (= *A. terrestris* (Savigny, 1826) *f. longa* Ude, 1855)
Allolobophora nocturna Evans, 1946
Allolobophora tuberculata Eisen (1874) (= *A. arnoldi* Gates, 1952)
Allolobophora chlorotica (Savigny, 1826)
Allolobophora limicola Michaelsen, 1890
Allolobophora rosea (Savigny, 1826) *f. typica* (= *Eiseneia rosea*)
Allolobophora rosea (Sav.) *f. macedonia*
Bimastos eiseni (Levinson, 1884)
Bimastos icenorum (Pickford, 1926)
Bimastos muldali Omodeo, 1956 (= *Allolobophora minima* Muldal, 1952)
Bimastos parvus (Eisen, 1784) (= *Bimastus beddardi* Michaelsen, 1894)
Dendrobaena mammalis (Savigny, 1826)
Dendrobaena octaedra (Savigny, 1826)
Dendrobaena pygmaea (Savigny, 1826)
Dendrobaena veneta (Rosa, 1886) *f. typica* (= *Eisenia veneta*)
Dendrobaena veneta (Rosa) var. *hibernica* (Friend, 1892) *f. typica*
Dendrobaena veneta (Rosa) var. *hibernica* (Friend) *f. dendroidea* (Friend, 1909)
Dendrobaena veneta (Rosa) var. *hortensis* (Michaelsen, 1890)
Dendrobaena veneta (Rosa) var. *zebra* (Michaelsen, 1902)
Dendrobaena rubida (Savigny, 1826) *f. typica*
Dendrobaena rubida (Sav.) *f. subrubicunda* (Eisen, 1874) (= *D. subrubicunda*)
Dendrobaena rubida (Sav.) *f. tenuis* (Eisen, 1874) (= *Bimastus tenuis*)
Eiseniella tetraedra (Savigny, 1826) *f. typica*
Eiseniella tetraedra (Sav.) *f. hercynia* (Michaelsen, 1890)
Eiseniella tetraedra (Sav.) *f. macrura* (Friend, 1892)
Eiseniella tetraedra (Sav.) *f. tetragonura* (Friend, 1892)
Eophila icterica (Savigny, 1826) (= *Allolobophora icterica*)
Helodrilus oculatus (Hoffmeister, 1845) (= *Eophila oculata*)
Lumbricus castaneus (Savigny, 1826)
Lumbricus festivus (Savigny, 1826)
Lumbricus friendi (Cognetti, 1904)
Lumbricus rubellus (Hoffmeister, 1845)
Lumbricus terrestris (Linnaeus, 1758)
Octolasion cyaneum (Savigny, 1826)
Octolasion lacteum (Oerley, 1881)

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